Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 38, No. 5, May 1981

Volume 38, nº 5, mai 1981

Canada

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Government of Canada
Fisheries and Oceans

Gouvernement du Canada
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Volume 38, No. 5, May 1981

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Canadian Journal of Fisheries and Aquatic Sciences

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Volume 38, No. 5, May 1981

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Life Table Evaluation of Chronic Exposure to a Pesticide

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DANIELS, R. E., AND J. D. ALLAN. 1981. Life table evaluation of chronic exposure to a pesticide. Can. J. Fish. Aquat. Sci. 38: 485–494.

The copepod *Eurytemora affinis* and the cladoceran *Daphnia pulex* were cultured at sublethal concentrations of dieldrin to test the usefulness of the intrinsic rate of population increase, r, as a bioassay statistic. The 48-h LC50 for *E. affinis* was 23 μg/L, but population growth rate measured by the life table method was only 12% of its control value at 5 μg/L and was zero at 10 μg/L, indicating a substantial sublethal effect. In contrast, *D. pulex* had a higher EC50 (251 μg/L) and showed little impairment of population growth potential below 220 μg/L. We suggest that the cladoceran was less sensitive than the copepod in both short- and long-term tests because of its simpler life cycle and larger size at hatching. The life table estimate of r appears to be an ecologically realistic measure of sublethal stress and requires an equivalent or shorter time to conduct than conventional long-term tests.

Key words: acute toxicity, chronic toxicity, life table, r, toxic substances, *Daphnia pulex*, *Eurytemora affinis*, pesticide, dieldrin

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Dans le but de vérifier l'utilité du taux intrinsèque d'augmentation de population, r, comme statistique d'essai biologique, nous avons cultivé le copépode *Eurytemora affinis* et le cladocère *Daphnia pulex* à des concentrations sublétales de dieldrine. La CL50 après 48 h de *E. affinis* est de 23 μg/L, alors que le taux de croissance de la population mesuré par la méthode de table de mortalité n'est que de 12% de sa valeur témoin à 5 μg/L et de zéro à 10 μg/L, signe d'un important effet sublétal. Par contraste, *D. pulex* a une CE50 plus élevée (251 μg/L) et son potentiel de croissance de population n'est pas affaibli au-dessous de 220 μg/L. Le cladocère serait moins sensible que le copépode dans les essais, tant à court terme qu'à long terme, à cause de son cycle biologique plus simple et de sa taille plus grande à l'éclosion. L'estimation de r par la table de mortalité semble être une mesure écologique-

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Printed in Canada (J6113)
Imprimé au Canada (J6113)

ment réaliste de stress sublétal et requiert un temps équivalent ou plus court que les essais conventionnels à long terme.

Received June 5, 1980
Accepted February 4, 1981

Reçu le 5 juin 1980
Accepté le 4 février 1981

ECOLOGISTS have used the life table since its introduction by Birch (1948) to assess survival, fecundity, and growth rate of populations under various environmental conditions. While it has proved a useful tool in analyzing the dynamics of natural populations, the life table approach has not, with few exceptions (Marshall 1962; Hummon 1974; Winner and Farrell 1976), been used as a toxicity bioassay. The principal summary statistic r is calculated from the equation of Lotka (1925)

$$(1) \quad \Sigma l_x m_x e^{-rx} = 1.$$

For a cohort of animals observed from birth through death at regular intervals (x), l_x is the probability of surviving to age x, and m_x represents the number of female offspring per female of age x, born during the time interval x to $x + 1$ (see Keyfitz 1968 for a thorough treatment). This statistic r, termed the intrinsic rate of natural increase, is the growth constant of an exponentially increasing population.

While short-term tests of acute toxicity (such as the concentration sufficient to kill 50% of the test animals in a specified time, LC50) are of value, there is increasing recognition of possible deleterious effects due to chronic exposure to lower concentrations (Sprague 1976; Scherer 1979). We hypothesize that r may be used as an ecological measure of chronic exposure to sublethal concentrations of a pesticide such as dieldrin (Fig. 1). If sublethal effects are minimal or nonexistent, curve I will be observed. At the other extreme, curve III describes a population with virtually no growth potential at a pesticide level well below the lethal concentration.

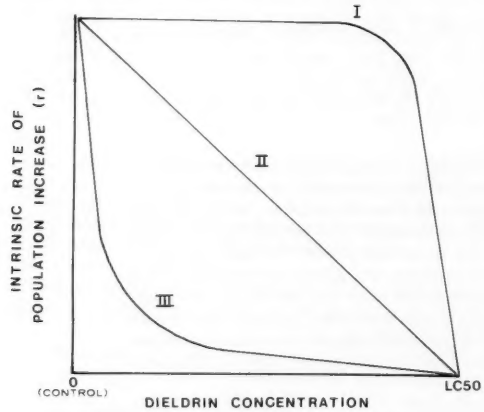

FIG. 1. Three possible hypotheses describing the effects of sublethal concentrations of any toxicant, illustrated by dieldrin, on the intrinsic rate of population increase r. Hypothesis I: no effect. Hypothesis II: the effect is proportional to the dieldrin concentration. Hypothesis III: there is a marked effect of dieldrin on r at sublethal concentrations.

The main purpose of this study was to examine the response of r to increasing concentrations of a toxic chemical. We chose a species of *Daphnia* because daphnid species are used routinely in toxicity testing. *Daphnia pulex* (Cladocera: Daphniidae) was studied rather than the commonly used *D. magna*. *Daphnia pulex* is widespread in North American ponds (unlike *D. magna* (Brooks 1957)) while still of sufficiently large size for easy handling. We also included a coastal copepod because (1) we believe there is no a priori reason why copepods and cladocerans should respond similarly, and (2) daphnids do not occur in coastal or marine waters where copepods are abundant, hence tests with copepods are needed. *Eurytemora affinis* (Copepoda: Calanoida) was selected as an easily cultured copepod which occurs in euryhaline coastal conditions (Katona 1970).

We chose the chlorinated hydrocarbon dieldrin, a pesticide in wide use in the United States until 1973, because of the extensive literature on the effects of this and related chemicals (Matsamura 1975). While no longer used in North America, dieldrin persists in the environment because of its slow degradation and probably is representative of other organochlorines presently in use, such as Mirex.

Methods and Materials

Eurytemora affinis

Eurytemora affinis cultures were obtained from Dr D. R. Heinle, Chesapeake Biological Laboratory, Solomons Island, Maryland, and had been maintained in the laboratory for at least 2 mo (three to four generations). The animals were maintained in filtered (0.45 μm Millipore), autoclaved, Chesapeake Bay water (salinity 8−10‰) at 18°C (± 1°C) on a 12-h photoperiod. *Eurytemora affinis* typically undergoes population expansion in Chesapeake Bay from February to May, as water temperatures warm from 5 to 15−20°C (Allan et al. 1976). A temperature of 18°C was chosen as representative of the upper range during which *E. affinis* develops. Stock and experimental animals were fed *Pseudoisochrysis* sp. and *Isochrysis* sp., two yellow-brown algae obtained from Horn Point Biological Laboratory, Horn Point, Maryland. The algae were grown in full-strength Provasoli's E.S. medium (Stein 1973) at 18°C (± 1°C) on a 16:8 light−dark cycle. The algae were maintained in log phase growth by transferring cultures to new medium every week.

Both acute and chronic bioassays were begun with newborn (± 24 h) nauplii obtained by isolating females bearing eggs from a mass culture. Forty-eight-hour acute bioassays were initiated with 20 nauplii at each concentration, five each in four 62 × 26 mm stendor dishes containing 20 mL of bay water. Nauplii used in acute tests were not fed. Nauplii were considered dead if no movement was observed at a magnification of 25×. The chronic bioassays were initiated with 60 nauplii for each test condition, six animals in each of 10

stendor dishes containing 20 mL of bay water. Dieldrin concentrations used were 0 (control), 1, 2, 3, 4, 5, and 10 μg/L. Because acetone was required as a carrier for dieldrin, an additional control, acetone only, was included. Its concentration was 10 μg/L, corresponding to the highest acetone concentration used in dieldrin experiments, and well within accepted levels for exposure to acetone (APHA 1976). Until an age of 15 d, sexes could not be distinguished and survivorship was based on both males and females. After day 15, a mating pair of copepods was isolated in one dish and thereafter survivorship was based on females only. Every other day, the water was changed and animals were fed 5×10^5 cells · mL^{-1}. Surplus algal cells were always observed still in suspension when the medium was changed. Algal concentrations were determined using a Klett Sommerson colorimeter with a No. 42 blue filter. The algae were concentrated by centrifugation at 200 rpm for 10 min.

Daphnia pulex

Daphnia pulex were collected from a mountain pond in West Virginia and identified according to Brooks (1957). Animals were maintained on a 12-h photoperiod in a defined medium (D'Agostino and Provasoli 1970) which included trace metals prepared according to Hutner (1972). A temperature of 20°C was chosen for *D. pulex* to facilitate comparison to previous work done mainly at this temperature, and because it occurs in ponds during the summer at 15−25°C (Allan unpublished data). Animals used for bioassays were at least the third generation raised in defined medium.

The daphnids were fed *Ankistrodesmus falcatus*, a green alga, grown in ASM-1 medium (Gorham et al. 1964) enriched with a modified vitamin supplement (Shiraishi and Provasoli 1959). *Ankistrodesmus falcatus* was maintained at 18°C in a chemostat on a 16-h photoperiod. The cells were maintained in log phase growth by removing 500 mL every other day and replacing this volume with new medium.

Both acute and chronic bioassays were begun with newborn (± 24 h) neonates obtained by isolating females bearing eggs from a mass culture. Forty-eight-hour acute bioassays were initiated with 20 neonates at each concentration, five each in four 50 × 45 mm jars containing 40 mL of medium. The animals were not fed. The EC50, the concentration at which 50% of the animals were effectively damaged, was used as the acute bioassay statistic. Effectively damaged is defined as the inability to move except for minor activity of the appendages (Sanders and Cope 1966). If no heart beat was observed at 25×, the animal was considered dead. Each chronic bioassay was begun with 23 neonates, one animal per jar containing 40 mL of medium. Dieldrin concentrations used were 0, acetone control (220 μg/L), 20, 50, 80, 120, 140, 180, 200, and 220 μg/L. Every other day, the medium was changed, young were discarded, and the animals fed $2.5-3.0 \times 10^5$ cells · mL^{-1}. Algae were observed in the guts of the daphnids throughout most of the experiment. Algal concentrations were determined as described for *E. affinis*.

Dieldrin Concentrations

The dieldrin used in these experiments was 99.9% pure as assayed by Shell Oil Co. A stock solution of 25 mg dieldrin in 25 mL of reagent-grade acetone was used to make all experimental solutions. A 10-μL (± 0.1 μL) Hamilton syringe was used for the *E. affinis* experiments to make a 10 μg/L solution from which all other concentrations were made by serial dilution. Dieldrin solutions of different concentrations for the *D. pulex* experiments were made by direct injection into 1-L flasks using 10- and 50-μL (± 0.1 μL) Hamilton syringes. The stock solution was replaced three times in the course of the experiment. On two occasions old and new solutions were compared using gas chromatography and no change in dieldrin concentration was observed. Hexane extraction and analysis on a Hewlett Packard 5840A gas chromatograph was used to determine whether a 1 μg/L dieldrin concentration remained in solution over a 3-d period.

Results

Analysis of variance showed that the concentration of dieldrin in a 1 μg/L solution did not vary significantly over a 3-d period. Mean percentage recovery was between 97 and 99%. The Chesapeake Bay water used for experiments contained no dieldrin or aldrin within the range of detection (5×10^{-5} μg/L).

Eurytemora affinis

The 48-h LC50 value for 1-d-old nauplii was determined experimentally to be 23 μg/L (95% confidence intervals 16.5−31.7). The LC50 value, confidence limits, and chi-square goodness of fit were determined by the method of Litchfield and Wilcoxson (1949).

Survivorship and fecundity — As both males and females were included in survivorship for days 1 through 18 and only females considered for day 18 through end of life, the two segments of the survivorship curves were analyzed separately. In control and low (1−4 μg/L) dieldrin concentrations, survivorship to day of first reproduction (day 18) ranged from 60 to 73%. In contrast, only 30−38% of the copepods raised at higher (5 and 10 μg/L) dieldrin concentration survived to this age (Fig. 2). A comparison by contingency table analysis of proportion surviving and not surviving showed a significant difference ($P < 0.001$) between populations maintained at 5 and 10 μg/L and all other populations.

After day 18, mortality was minimal or zero for the next 12−18 d in all experimental groups except 10 μg/L (Fig. 2). Mortality then increased again in all experiments due to senescence, and perhaps also due to accumulation of dieldrin in animals subjected to different concentrations. The Kruskal−Wallis nonparametric test ranking day of death revealed a significant difference among treatments ($P < 0.05$). Some major demographic trends derived from the *E. affinis* life tables are shown in Table 1. In general, total number of offspring produced, mean longevity, and total number of broods all decreased with increasing pesticide concentration. However, animals exposed to 1 μg/L had greater longevity, more young, and more broods than did control animals.

Day of first reproduction compared among treatments by the Kruskal−Wallis test showed significant differences ($P < 0.05$). A posteriori comparison based on rank sum ($\alpha = 0.05$) (Hollander and Wolfe 1973) showed that animals

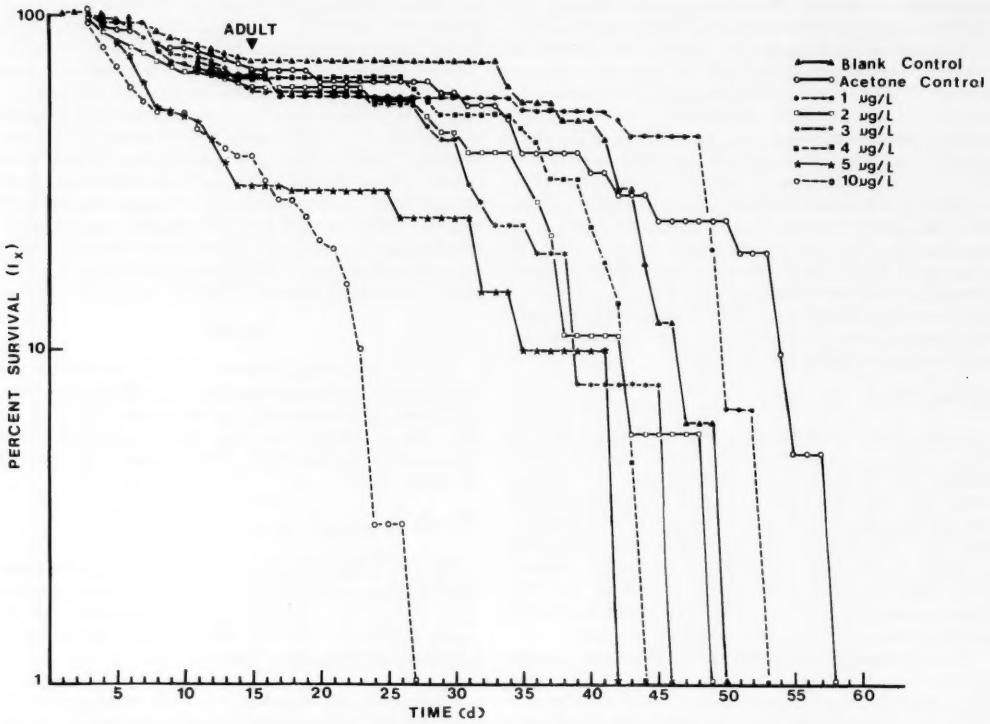

FIG. 2. Survivorship curves for *E. affinis* in six concentrations of dieldrin and two controls. $N = 60$ on day 1.

TABLE 1. Demographic information for *Eurytemora affinis* from life table experiments at various dieldrin concentrations. Standard deviations where indicated. Temperature was 18°C in all experiments.

Dieldrin concn. (µg/L)	Mean longevity (d)	Mean day of first reproduction	Maximum longevity (d)	Total no. of young	Total no. of broods	Mean brood size	Nos. of females in life table[b]
Blank control	41.0±5.07	18.1±.46	50	2467	91	27.1±12.4	12
Acetone control	42.5±11.2	19.2±1.7	58	3545	115	30.8±15.3	13
1	47.4±4.5	17.1±3.1	53	3708	135	27.5±12.5	15
2	35.3±6.5	20.4±1.3	49	1014	48	21.1±13.3	10
3	34.1±5.0	19.2±1.2	46	2173	81	26.8±12.2	15
4	37.3±5.5	19.4±2.1	44	1706	81	21.1±10.8	14
5	34.8±5.7	25±3.26	42	78	5	15.6±8.2	6 (of which only 3 reproduced)
10	27[a]	—	27	0	0	0	1

[a]Mean longevity and maximum longevity are the same since only one female survived in this concentration. This female died before reproducing.

[b]At day 18 when sex may be determined.

in blank control reproduced earlier than those in 2 and 5 µg/L, while those in 1 µg/L reproduced earlier than those in 2, 4, and 5 µg/L.

Fecundity curves tended to increase initially, stay high for a variable period, then decline as the animals aged (Fig. 3). Fecundity curves for control and 1 µg/L were roughly similar and showed greater fecundity than was observed at 2 through 5 µg/L. Peak fecundity for both controls and at 1 µg/L was 11 female offspring · adult female^{-1} · d^{-1}, compared to 3–6 female offspring · adult female^{-1} d^{-1} at higher dieldrin con-

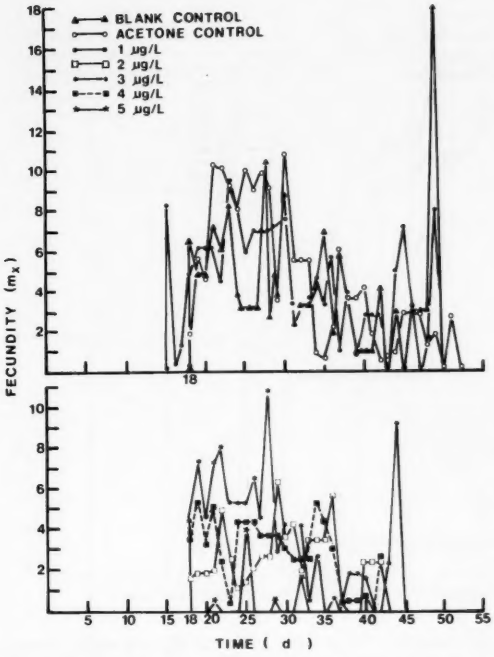

FIG. 3. Fecundity curves (m_x) for *E. affinis* in two controls and 1, 2, 3, 4, and 5 µg/L dieldrin.

centrations. Last day of reproduction ranged from day 50 through 52 for the former and from day 42 through 45 for the higher concentrations.

Dieldrin lengthened development time to reproductive maturity at 5 and 10 µg/L concentrations. While adult males and females were recognizable in all other concentrations by day 15 and reproduced by day 18, only three of the six surviving females in 5 µg/L were recognizable as females by day 18, and the other three by day 21. The mean day of first reproduction was day 25 (Table 1). In 10 µg/L the one surviving female was not recognizable as such until day 23. This female developed ovaries but died before reproducing.

Analysis of variance of brood sizes showed no significant difference among the pesticide treatments. The maximum number of broods produced decreased as the concentration increased (Table 1) because female survivorship decreased. The maximum number of broods produced in the acetone control, blank control, and 1 µg/L was 14, 12, and 14, respectively, while 7, 8, and 9 broods were produced in 2, 3, and 4 µg/L, respectively. Two broods were produced in 5 µg/L.

Intrinsic rate of population increase (r) — The intrinsic rate of population increase r showed little change with increasing dieldrin concentration until 5 µg/L. It then declined drastically (Fig. 4), as did survivorship, fecundity, and number of broods (Fig. 2, 3, and Table 1). The r value for 10 µg/L is equal to zero since reproduction did not occur

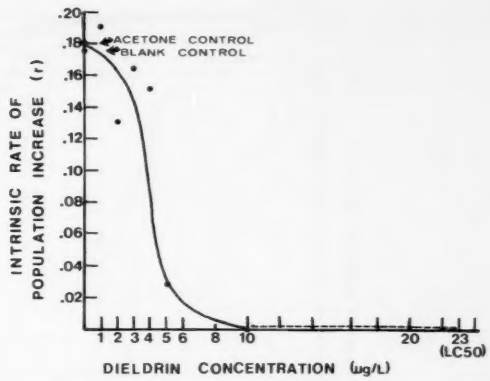

FIG. 4. The intrinsic rate of population increase, r, for *E. affinis* plotted against experimental dieldrin concentrations.

at this concentration. At 5 µg/L, which is 20% of the experimentally determined LC50, r was 12% of its control value.

Daphnia pulex

The 48-h EC50 concentration for *D. pulex* was determined to be 251 µg/L (95% confidence intervals 217.4–290.1). EC50 value, 95% confidence limits, and goodness of fit were determined by the method of Litchfield and Wilcoxson (1949).

Survivorship and fecundity — Survivorship decreased significantly with increasing concentration of dieldrin, particularly above 100 µg/L (Fig. 5). Survivorship curves were analyzed using the Kruskal–Wallis test, with day of death as the ranked observation. A posteriori comparison of survivorship curves was accomplished using rank sums (Hollander and Wolfe 1973). Survivorship at 120, 140, 180, 200, and 220 µg/L was significantly different from 80 µg/L and all lower concentrations ($\alpha = 0.05$, Table 2). Survivorship at 100 µg/L was significantly different from survivorship at 200 and 220 µg/L.

Some major demographic trends observed in the *D. pulex* experiments are shown in Table 3. There was a trend for mean longevity, total young, and number of broods produced to decline with increasing dieldrin concentration. These conclusions unfortunately must be qualified owing to a small temperature increase which affected experiments at higher dieldrin concentrations (Table 3). This magnitude of a decrease in fecundity is not expected from a small temperature increase, however, and presumably is due to increasing levels of dieldrin.

Day of first reproduction was compared statistically by the same method as described for *E. affinis*. Although variable, the general trend is for a significantly earlier day of first reproduction for the acetone control, 140, 180, 200, and 220 µg/L (Table 3). This decrease may be explained by the fact that organisms in these concentrations experienced slightly higher mean temperatures (22.5°C vs. 20°C) due to inadequate temperature control.

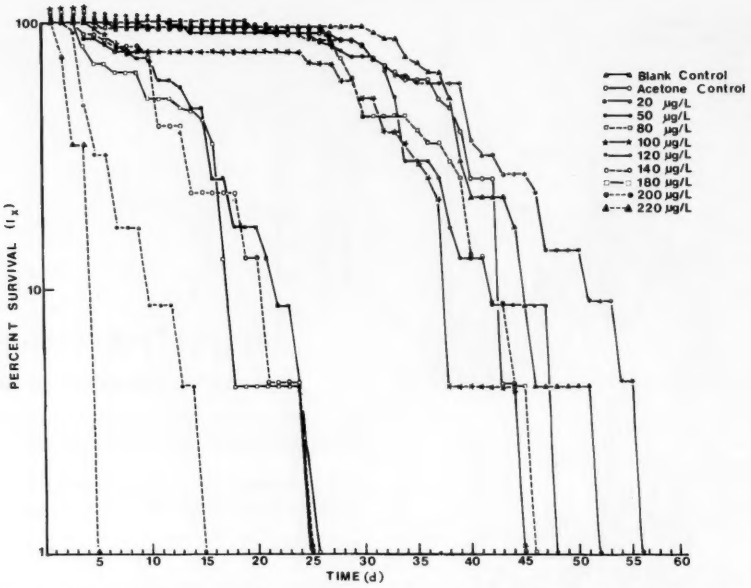

FIG. 5. Survivorship curves for *D. pulex* in 10 concentrations of dieldrin and two controls. $N = 23$ on day 1.

Mean brood sizes were compared after weighting the mean for each pesticide concentration by the reciprocal of its variance to correct for heterogeneity of variance (Sokal and Rohlf 1969). Mean brood sizes were not significantly different (Table 3). The fecundity curves for *D. pulex* showed considerable variation; in general, the only trend attributable to dieldrin was that reproduction ended sooner at higher concentrations (Fig. 6). Fecundity curves and total number of broods both decreased with increasing dieldrin concentration because female survivorship was reduced (Fig. 5).

Intrinsic rate of population increase (r) — The intrinsic rate of population increase did not decline markedly until dieldrin concentration exceeded 180 µg/L (Fig. 7). The slightly higher temperatures at which some (mostly high) dieldrin treatments were tested led to significantly earlier reproduction (Daniels 1979); this in turn may have compensated for the effect of higher mortality which would reduce r. To assess this possibility, we recalculated r for the dieldrin treatments where higher temperatures occurred, by correcting day of first reproduction to its typical value in our 20°C experiments. These results indicate minor reduction in r in the 0−180 µg/L range (stars in Fig. 7). However, the major conclusion remains unchanged: dieldrin concentrations up to 70% of the 48-h EC50 had only minor effects on reproductive capabilities. At 200 µg/L, however, r was severely reduced and at 220 µg/L, $r = 0$ since all animals died before reproducing.

Discussion

The intrinsic rate of population increase r integrates age at first reproduction, survivorship, brood size and frequency, and longevity. Therein lies its desirability as a single estimate of the capability of a population to grow under chronic exposure to a particular level of some toxicant. However, it is also of value to examine how chronic exposure affects the individual components of r.

A delay in age at first reproduction would be expected to reduce population growth capacity more seriously than would a decrease in brood size or longevity (Cole 1954; Lewontin 1965; Allan 1976). For *E. affinis*, exposure to dieldrin levels well below the LC50 significantly reduced the proportion of individuals surviving to reproductive maturity and delayed the onset of reproduction (Fig. 2, 3, Table 1). These effects were more important than the slightly impaired fecundity in reducing r. In contrast, *D. pulex* showed a significant shortening of the time to first reproduction with increasing pesticide levels (Table 3). As the amount of change is roughly what would be expected (Allan 1976) for the slightly higher temperatures which accompanied the higher dieldrin levels, there probably was little effect of dieldrin on age at first reproduction. *Daphnia pulex*, as with *E. affinis*, showed no marked response in brood size (Table 3). Although Marshall (1978) and Winner and Farrell (1976) both reported daphnids to show an increase in mean brood size with increasing toxic stress, thus producing a compensatory effect, we did not observe such an effect. The principal manner in which dieldrin affected *D. pulex* was through decreased survivorship to reproductive maturity (Fig. 5).

In summary, exposure to low concentrations of dieldrin reduced survivorship, but had little effect on reproduction of those surviving, in both test animals. Chronic exposure also delayed the onset of reproduction in *E. affinis* and probably did not do so for *D. pulex*, although inadequate temperature

TABLE 2. Comparison of survivorship curves for *D. pulex* accomplished using the Kruskal–Wallis test. Day of death was used as the ranked observation. Multiple comparison between treatments was based on ranked sums (Hollander and Wolfe 1973). Asterisks show a significant difference between treatments ($P < 0.05$). Concentrations in μg/L. AC, acetone control; BC, blank control.

	BC	AC	20	50	80	100	120	140	180	200	220
BC											
AC											
20											
50											
80											
100											
120	*	*	*	*	*						
140	*	*	*	*	*						
180	*	*	*	*	*						
200	*	*	*	*	*	*			*		
220	*	*	*	*	*	*			*		

TABLE 3. Demographic trends for *D. pulex* summarized from life tables. Standard deviations where indicated.

Dieldrin concn. (μg/L)	Mean longevity (d)	Mean day of first reproduction	Maximum longevity (d)	Total no. of young	Total no. of broods	Mean brood size	Mean temp. of exp. (°C)
Blank control	37.5±7.8	9.8±1.6	52	2461	230	10.7±5.3	20±1
Acetone control	35.6±8.4	8.4±0.7	45	2883	240	12.0±6.8	21.5±0.5
20	38.4±9.5	10.5±1.0	56	2540	219	11.6±5.6	20±1
50	33.7±7.7	9.1±1.0	48	2460	206	11.9±6.0	20±1
80	32.3±7.8	11.5±1.0	48	2410	204	11.8±4.9	20±1
100	27.4±12.2	9.4±0.9	45	2140	188	11.4±4.6	20±1
120	13.7±6.1	8.8±0.4	25	631	57	11.1±5.4	21.5±0.5
140	13.0±4.9	7.6±0.7	25	609	61	10.0±5.2	22.5±0.5
180	13.1±5.6	8.0±0.4	26	662	57	11.6±4.6	22.5±0.5
200	5.7±3.0	8.3±0.6	15	70	6	11.7±5.4	22.5±0.5
220	3.4±1.2	0	5	0	0	0	22.5±0.5

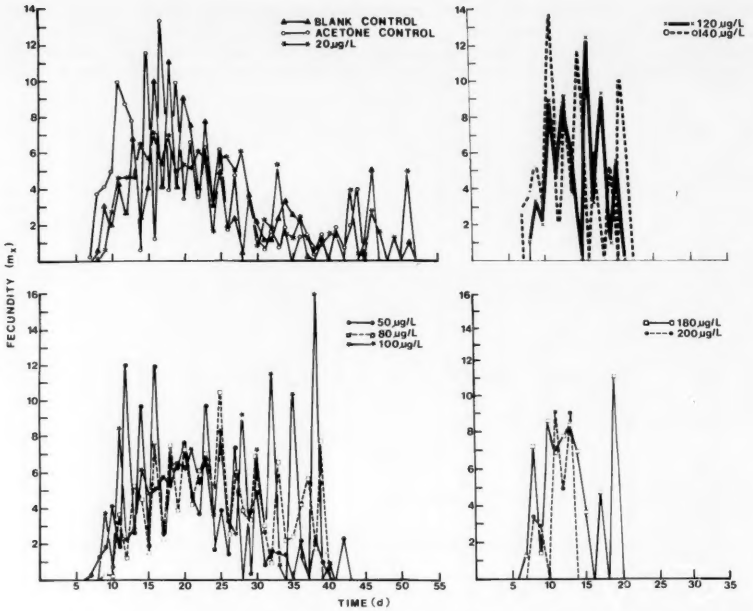

FIG. 6. Fecundity curves (m_x) for *D. pulex* in two controls and 20, 50, 80, 100, 120, 140, 150, 180, and 200 µg/L dieldrin.

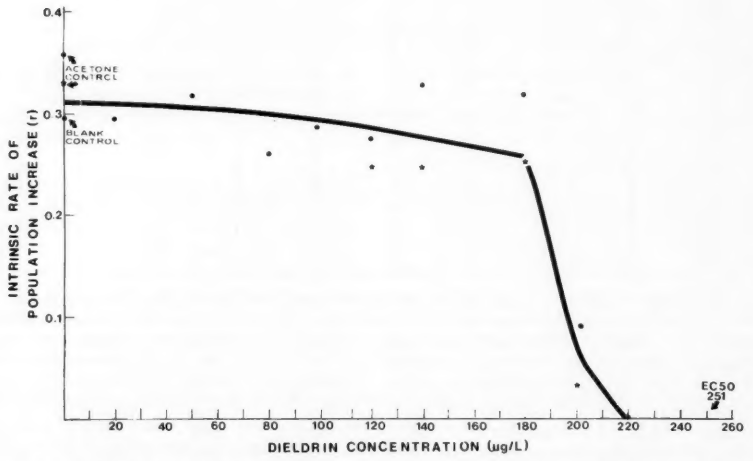

FIG. 7. The intrinsic rate of population increase *r* for *D. pulex* plotted against experimental dieldrin concentrations. Stars represent values recalculated to correct for a small temperature increase which affected higher dieldrin concentrations.

control compromises this last result.

Eurytemora affinis and *D. pulex* differed markedly in their sensitivity to dieldrin. The LC50 value of the former was 9.2% of the EC50 value of the latter. The intrinsic rate of increase of *E. affinis* clearly shows a "type III" response to increasing dieldrin concentration, as *r* was very substantially reduced at a level of toxicant only 20% of the LC50 value. In contrast, *r* of *D. pulex* did not appear to be affected until

TABLE 4. Comparison of this study with three other studies comparing LC50 and intrinsic rate of population increase r.

Species	Reference	Toxicant	LC50 (μg/L)	r[a] (μg/L)	Hypothesis
E. affinis	This study	Dieldrin	23	5	III
D. pulex	This study	Dieldrin	251	200	I
D. pulex	Winner and Farrell (1976)[b]	Copper	70	60	I
D. magna	Winner and Farrell (1976)[b]	Copper	86.5	80	I
D. parvula	Winner and Farrell (1976)[b]	Copper	64.5	60	I
D. ambigua	Winner and Farrell (1976)[b]	Copper	67.7	60	I
D. magna	Winner et al.[b] (1977)	Copper (Alga diet)	87	80	I
D. magna	Winner et al.[b] (1977)	Copper (Trout chow)	83.4	60	III
Lepidodermella sqummata	Hummon (1974)	DDT	9000	500	III

[a]The level of toxicant shown is that concentration where r was first affected.
[b]Seventy-two-hour LC50.

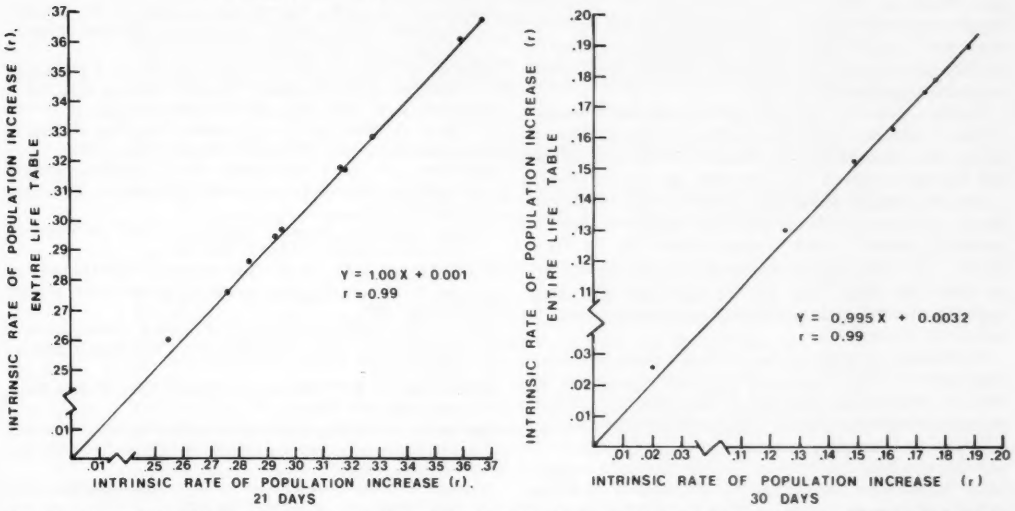
INTRINSIC RATE OF POPULATION INCREASE (r), ENTIRE LIFE TABLE
Y = 1.00 X + 0.001
r = 0.99
INTRINSIC RATE OF POPULATION INCREASE (r), 21 DAYS
INTRINSIC RATE OF POPULATION INCREASE (r) ENTIRE LIFE TABLE
Y = 0.995 X + 0.0032
r = 0.99
INTRINSIC RATE OF POPULATION INCREASE (r) 30 DAYS

FIG. 8. *Left panel*: Correlation of the intrinsic rate of population increase r for *D. pulex* calculated for the duration of the life table and after 21 d. *Right panel*: Correlation of the intrinsic rate of population increase r for *E. affinis* calculated for the duration of the life table and after 30 d.

exposed to a toxicant level $\simeq$ 80% of the EC50. This "type I" response would appear to justify acute tests, while at least for *E. affinis*, an acute test would have been woefully inadequate.

Some explanation of the difference in response of the two test organisms is suggested by a comparison of their life histories. *Eurytemora affinis* has a dry weight of $\sim$ 0.15 μg as a nauplius I, 8 μg as an adult (Heinle 1966), and requires $\sim$ 15 d to mature at the experimental temperature. *Daphnia pulex* weighs $\sim$ 3 μg as a neonate, 30 μg as an adult (Richman 1958), and requires 8–10 d to mature at test temperatures. Clearly *E. affinis* is exposed for a longer time and at a smaller size, hence at a greater surface:volume ratio. In addition, copepods experience 11 prereproductive molts and considerable morphological reorganization, compared to four to five simple instar molts for daphnids. However, until further life table studies of both cladocerans and copepods are conducted, such interpretations must be viewed as speculative.

Although the intrinsic rate of increase of *D. pulex* was not sensitive to chronic exposure to dieldrin concentrations at or below 200 μg/L (Fig. 7), survivorship clearly was reduced at concentrations in excess of 100 μg/L (Fig. 5). Thus at pesticide levels less than half the EC50, a measurable response

was obtained from the organism. Whether this is ecologically relevant to the ability of a population in nature to sustain itself is questionable, as r was little affected. However, the effect of decreased survivorship on r was offset by higher temperatures accompanying higher dieldrin treatments discussed above. Thus for these experiments with *D. pulex*, r may have underestimated the potential ecological impact of chronic exposure to dieldrin.

Other studies which compare an LC50 value and the response of r to various toxicant levels are presented in Table 4. Winner and Farrell (1976) and Winner et al. (1977) examined copper toxicity to several species of *Daphnia* and compared two diets. Of six experimental combinations, five supported hypothesis I. Only *D. magna* fed trout chow showed a type III response, and a delay in the onset of reproductive maturity. In addition, Hummon (1974) found a type III response in gastrotrich *Lepidodermella squammata* exposed to DDT. A decrease in the number of individuals producing eggs and the number of eggs produced per individual as well as a marked increase in time to hatching of first brood all contributed to a decrease in r well before the LC50.

Daphnia is widely used as a "typical" aquatic test organism. Based on these limited comparisons, its sensitivity appears not to differ greatly between long-term and short-term tests. Yet *E. affinis* clearly differs, raising concern about the applicability of results of short-term LC50 tests with *Daphnia* to aquatic organisms in general.

Finally, while the life table method and the population statistic r meet the biological objectives of chronic bioassay testing, this approach may be criticized for the long duration and expense involved. To determine the feasibility of a shorter test, portions of the original data set were reexamined. For *D. pulex* the correlation between r calculated after 21 d and for the entire life table is nearly perfect (Fig. 8). For *E. affinis*, a 30-d test gives an estimate of r nearly identical with the entire life table. Thus, the life table approach can be applied confidently to data collected over only a portion of the organism's entire life.

A potential limitation of this approach is the absence of information on the survival and reproduction of young produced by test animals. Marshall (1978) observed significant postnatal mortality at elevated concentrations of cadmium. In addition, as Marshall points out, in situ experiments are required as a final link between the laboratory and events in lakes. Nonetheless, we believe the life table is of demonstrated usefulness as a laboratory bioassay for short-lived test organisms, such as aquatic invertebrates, and deserves further investigation.

Acknowledgments

We are grateful to Sherry Morris for technical assistance, Judd Nelson for aid in pesticide techniques, and Estelle Russek for statistical advice. Comments by reviewers on an earlier version improved the manuscript. This research was supported by a grant from the Office of Water Research and Technology, USDI.

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Temporal Changes in the Reproductive Potential of Female Harp Seals (*Pagophilus groenlandicus*)

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The Northwest Atlantic harp seal (*Pagophilus groenlandicus*) population declined by more than 50% between 1952 and the early 1970s. Biological sampling of female reproductive tracts began in 1951 and has continued to the present. We reexamined the extent to which mean age of maturity and fertility rate have changed as population size declined. Mean age of maturity declined from ~6.2 yr in 1952 to 4.5 yr in 1979. During this same period fertility rate increased from 85 to 94%. Both parameters have changed concurrently with a decline in numbers. Although it is likely that density-dependent mechanisms are involved, empirical data are lacking.

Key words: harp seals, *Pagophilus groenlandicus*; maturity, fertility, density-dependence

BOWEN, W. D., C. K. CAPSTICK, AND D. E. SERGEANT. 1981. Temporal changes in the reproductive potential of female harp seals (*Pagophilus groenlandicus*). Can. J. Fish. Aquat. Sci. 38: 495–503.

Entre 1952 et le début des années 1970, la population de phoques du Groenland (*Pagophilus grœnlandicus*) de l'Atlantique nord-ouest diminua de plus de 50%. L'échantillonnage biologique du tractus reproducteur des femelles commença en 1951 et s'est poursuivi jusqu'à ce jour. Nous avons réexaminé l'étendue des changements qui se sont produits dans l'âge moyen de maturité et dans le taux de fertilité à mesure que diminuaient les effectifs de la population. L'âge moyen de maturité diminua, passant d'environ 6,2 ans en 1952 à 4,5 ans en 1979. Pendant cette même période, le taux de fertilité augmenta, passant de 85 à 94%. Les deux paramètres ont changé en même temps que la diminution des effectifs. Il est probable que des mécanismes dépendant de la densité soient impliqués, mais nous n'avons pas de données empiriques pour le démontrer.

Received July 16, 1980
Accepted January 28, 1981

Reçu le 16 juillet 1980
Accepté le 28 janvier 1981

ANIMAL populations often exhibit changes in reproductive parameters following marked changes in population size. Two of these parameters, fertility rate and mean age of sexual maturity, are of particular interest with respect to the management of Northwest Atlantic harp seals, *Pagophilus groenlandicus*.

A period of heavy commercial exploitation reduced the 1+ population size of harp seals in the Northwest Atlantic by more than 50% between 1952 and the early 1970s (Lett et al. 1978; Winters 1978). These analyses also suggested that since the introduction of quotas in 1972, population size has stabilized and may be slowly increasing. Biological sampling of female harp seal reproductive tracts began in 1951 and has continued to the present. Thus it is possible to follow changes in reproductive parameters as the population declined.

Sergeant (1966, 1973, 1976, 1978) concluded that mean age of whelping of female harp seals declined concurrently with population size, but that the fertility rate of older

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Printed in Canada (J6156)
Imprimé au Canada (J6156)

TABLE 1. Reproductive samples of harp seal females collected in January–February from the Gulf and Front.

	1951–54: Fisher (1954)					1964						1965					
Age in years	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.
1						3	3										
2	1	1				8	8					7	7				
3	5	5				16	16					18	18				
4	4	4				11	11					30	29	1		0.03	0.03
5	3	2	1		0.33	9	7	1	1	0.22	0.22	44	39	5		0.11	0.11
6	3	1	2		0.67	2		1	1	1.00	0.50	37	16	20	1	0.57	0.57
7	16	1	12	3	0.94	4	1	3		0.75	0.75	38	11	27		0.71	0.71
8	4		3	1	1.00	5		5		1.00	1.00	33	1	28	4	0.97	0.97
9	8		7	1		4		4				15	1	12	2	0.93	0.99
10	8		7	1		2		1				5		5		1.00	1.00
11	4		4			1		1				5		5			
12	3		3			6		5	1			10		10			
13						1		1				7		5	2		
14	2		2			1		1				8		8			
15+	4		3	1		6		4	2			26		23	3		
Total	65	14	44	7		79	46	27	6			283	122	149	12		
Fertility rate				86.3%					81.8%						92.6%		

84.6% from Fisher (1952)
(No details provided, $N = 133$)

	1966						1967						1968					
Age in years	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.
1	3	3					6	6					4	4				
2	11	11					7	7					12	12				
3	10	10					14	14					24	24				
4	7	7					10	10					27	27				
5	9	8	1		0.11	0.11	19	15	4		0.21	0.21	19	13	6		0.32	0.32
6	17	11	6		0.35	0.35	33	13	20		0.61	0.61	20	6	14		0.70	0.70
7	11	3	8		0.73	0.73	29	1	28		0.97	0.97	12	1	11		0.92	0.92
8	8	1	7		0.86	0.86	23	3	20		0.87	0.99	11	1	9	1	0.91	0.98
9	4	1	3		0.75	0.98	19	2	16		0.89	0.99	4		4		1.00	1.00
10	5		5		1.00	1.00	18	4	14		0.78	1.00	5		5			
11	4		4				11	1	10		0.91		4		3	1		
12	4		4				4		4		1.00		5		3	2		
13	6	1	5				5		4	1			3		3			
14	2		2				12		12				6		6			
15+	16	2	13	1			32	2	29	1			17		15	2		
Total	117	58	58	1			241	78	161	2			173	88	79	6		
Fertility rate				98.0%						98.8%						92.9%		

	1969						1970					1978					
Age in years	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.
1	4	4										6	6				
2	5	5					4	4				13	13				
3	20	20					6	6				32	32				
4	25	24	1		0.04	0.04	13	13				40	39	1		0.03	0.03
5	25	21	4		0.16	0.16	13	10	3		0.23	38	15	23		0.61	0.61
6	16	9	7		0.44	0.44	12	6	6		0.50	20	2	18		0.90	0.90
7	28	5	23		0.82	0.82	10	1	9		0.90	9	3	6		0.67	0.98
8	29	2	27		0.93	0.93	19	1	18		0.95	10	1	7	2	0.90	1.00
9	22		21	1	1.00	1.00	21	1	18	2	0.95	9		8	1	1.00	
10	17	1	16		0.94		12		12		1.00	7		7			
11	17	1	14	2	0.94		4		4			3		3			
12	9		9		1.00		8	2	6			1		1			
13	12	3	9				4	1	3			2		2			
14	11	1	10				6	1	4	1		2		2			
15+	47	5	40	3			33	3	27	3		7		5	2		
Total	287	101	180	6			165	49	110	6		199	111	83	5		
Fertility rate				96.8%						94.8%					94.3%		

TABLE 1. (*Concluded*)

	St. Anthony 1979				Combined St. Anthony–St. Lawrence estuary 1979 samples				
Age in years	*n*	Imm	Preg.	Mature non-preg.	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature
1	7	7			12	12			
2	18	18			27	27			
3	18	16	2		33	31	2		0.06
4	9	6	3		21	16	5		0.24
5	9	3	5	1	15	6	8	1	0.60
6	3		3		5		5		1.00
7	4		3	1	9		8	1	
8	2		2		4		4		
9	1		1		3		3		
10	1		1		2		2		
11					1		1		
12	1		1		2		2		
13	1		1		1		1		
14	1		1		2		2		
15+	4		3	1	6		5	1	
Total	80	50	27	3	143	92	48	3	
Fertility rate				90%				94.1%	

(age 8+) females had not changed. Lett and Benjaminsen (1977) and Lett et al. (1978) argued that both of these parameters changed with changing density. Winters (1978) agreed with Sergeant, claiming that mean age of whelping alone was density-dependent. Both authors argued that the conclusions of Lett et al. were an artifact resulting from the combination of early and late pregnancy rates. This introduces a bias since early pregnancy rates are always equal to or greater than late pregnancy rates.

There is sufficient confusion and misinterpretation of the data in the literature to warrant a new, more critical analysis. From the present analyses we conclude that both mean age of sexual maturity and fertility rate have changed significantly over the period 1950–79, but that the data are insufficient to determine the exact pattern of change over time or the underlying mechanisms responsible for this change. Although, both parameters have changed concurrently with a decline in population size, empirical data are lacking to substantiate the density-dependent effect.

Materials and Methods

The present analyses were based on female reproductive tracts and jaws collected during the spring (late March–April) or winter period (January–February) at various times from 1951 to 1979. These samples, their origin, and author source are given in Tables 1 and 2.

In all samples, age was determined to the nearest year by the method of counting dentine annuli described by Fisher (1954). For samples taken in April this is actual age less 1 mo, whereas for January–February samples this is actual age plus 1 or 2 mo. Briefly, a lower canine tooth is cross-sectioned ($\approx$100 μm) just below the gum line and the dentine of the section examined for annuli under a binocular microscope. Each section is examined only once and thus age is based on this one "reading." This method of age determination is not without error. Doubleday and Bowen (1980) have shown that aging errors tend to result in overestimated mean age of maturity. However, the conclusions of our analysis are unaffected by this potential bias.

The reproductive condition of females was assessed by examination of serially sectioned ovaries and where possible by gross examination of the uterus. Immature females have small ovaries containing only small inactive follicles and no corpus luteum or corpus albicans. Ovaries of females taken in April contain a luteinizing corpus luteum and no regressing corpus luteum or corpora albicantia, if the female has ovulated for the first time, or at least one corpus albicans or regressing corpus luteum if she is mature but not pregnant (Fisher 1954). It is possible that a small number of females will not have ovulated at the time of sampling in April. In most cases, however, this will indicate failure to ovulate rather than late ovulation. Fisher (1954) found that males sampled after March 28 showed a decrease in spermatogenic activity indicating that the end of mating probably occurs in early April. Thus, it is unlikely that many females would ovulate after this date. In January samples, the corpus luteum will be larger and fully luteinized if the female is pregnant or will have begun to degenerate if conception did not occur or if the fetus was aborted.

Fertility rate was defined as the percentage of mature females that are pregnant at the time of the sample. Because implantation of the blastocyst is delayed likely for about 2 or 3 mo after fertilization (Fisher 1954), fertility rate is easily measured only after implantation has occurred, that is, in winter samples. Using April samples ovulation rate was estimated as the percentage of mature females that had ovulated at the time of the sample. Thus, January and April samples should not be directly combined for the estimation of fertility rates.

Mean age of sexual maturity was determined using the algorithm of DeMaster (1978) as follows:

$$(1) \quad f(x) = t(x)/n(x)$$

where x = age of female, $f(x)$ = estimated probability of

TABLE 2. Reproductive samples of harp seal females collected in April from molting herds on the Front.

	1953; Fisher (1954) (only April samples used)					1952–54; Sergeant (1966)					1961–62; Sergeant and Khuzin combined; Sergeant (1966)				
Age in years	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature
1	4	4				3	3				15	15			
2	1	1				3	3				12	12			
3	12	12				6	6				8	7	1		0.13
4	13	13				3	3				14	7	7		0.50
5	17	11	6		0.35	6	4	2		0.33	10	4	6		0.60
6	6	2	4		0.67	10	3	7		0.70	9	1	8		0.89
7	4	1	3		0.75	8		8		1.00	11		11		1.00
8	2		2		1.00	6		6							
9	3		3			8		8			2		2		
10	2		2			3		3							
11	1		1			6		6			1		1		
12	2		2			2		2							
13	2		2			3		3							
14						1		1			2		2		
15+	4		4			7		5	2		5		5		
Total	73	44	29			75	22	51	2		89	46	43		
Ovulation rate			100%						96.2%					100.0%	

1966 (Sample taken in Gulf of St. Lawrence)						1968–70					1976					1979					
Age in years	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	*n*	Imm.	Preg.	Mature non-preg.	Fraction mature	Smoothed fract. mat.
1	9	9				36	36				20	20				69	69				
2	16	16				10	10				27	27				38	38				
3	10	10				10	9	1		0.10	15	15				16	16				
4	10	9	1		0.10	14	8	6		0.43	5	4	1		0.20	23	9	13	1	0.61	0.61
5	10	4	6		0.60	11	1	10		0.91	4	1	3		0.75	16	1	15		0.94	0.94
6	14	3	11		0.79	5		5		1.00	7	1	6		0.86	8	1	7		0.88	0.99
7	11		11		1.00	14		14			7		7		1.00	4		4		1.00	1.00
8	4		4			7		7			7		7			6		6			
9	1		1			6		6			11		11			3		3			
10	3		3								9	1	8			3		3			
11	5		5			2		2			1		1			4		4			
12	4		4								6		6			2		2			
13	2		2			2		2			5		5			2		2			
14	2		2			1		1			5		5								
15+	17	2	15			8		6	2		26	2	23	1		5		5			
Total	118	53	65			126	64	60	2		156	71	84	1		199	134	64	1		
Ovulation rate			100%						95.8%					98.8%					98.0%		

ovulating at or before age x, $t(x)$ = number of females of age x in the sample which have ovulated, and $n(x)$ = number of females age x in the sample. Thus, the estimated probability of first ovulating at age x is

$$(2)\quad P(x) = f(x) - f(x-1).$$

The average age of sexual maturity is then

$$(3)\quad \bar{x} = \sum_{x=0}^{w} (x)\,P(x)$$

where $\bar{x}$ = average age of sexual maturity and w = maximum age in the sample. The estimated variance for $\bar{x}$ is

$$(4)\quad v(\bar{x}) = \sum_{x=0}^{w-1} \frac{f(x)[1-f(x)]}{n_x - 1} + \frac{w^2 f(w)[1-f(w)]}{n(w)-1}$$

This estimate assumes that all of the $f(x)$'s are independent of each other. The 95% confidence intervals can be approximated by

$$(5)\quad 95\%\ \mathrm{CI} = \bar{x} \pm 1.96\,[v(\bar{x})]^{1/2}.$$

To obtain mean age of first whelping, 1 yr must be added to the values in Fig. 1 and 3 and Table 3.

This algorithm (DeMaster 1978) assumes that the probability of first ovulation at or before age x is a monotonically increasing series. In those samples where this was not the case, the series were smoothed to approximate a cumulative normal distribution (Tables 1 and 2). Smoothing was only necessary as the series became asymptotic to unity. Numbers at age are generally smaller in older age-classes and one animal incorrectly classified as to maturity or age is sufficient to cause a decrease in the fraction mature in the series. In single-observer age determination (using counts of dentinal annuli) the accuracy of age estimation is sensitive to the number of readings taken (Doubleday and Bowen 1980).

This approach to smoothing the age at sexual maturity data is based on the assumptions that all female seals eventually become sexually mature, and that the relationship between age and the probability of first ovulation at or before that age is sigmoid, approximating a Gaussian normal distribution.

In the statistical analyses of mean age at maturity all linear regressions were weighted by the numbers of females in the sample which contributed information to the calculation; e.g. for the 1964 sample in Table 1 the weighting would be $11 + 9 + 2 + 4 + 5 = 31$. Regressions predicting fertility rates were weighted by the number of sexually mature females in the sample.

Results

Age at Sexual Maturity

There were significant linear regressions of mean age of sexual maturity (MAM) against year for females sampled in April ($P = 0.011; r = -0.870, P = 0.011$) (Fig. 1A) and in January ($P = 0.011$; $r = -0.760$, $P = 0.011$) (Fig. 1B). Because the slopes and intercepts of these regressions are not significantly different, there is no statistical (or biological) reason why the maturity data from the two time periods should not be combined. The resulting regression

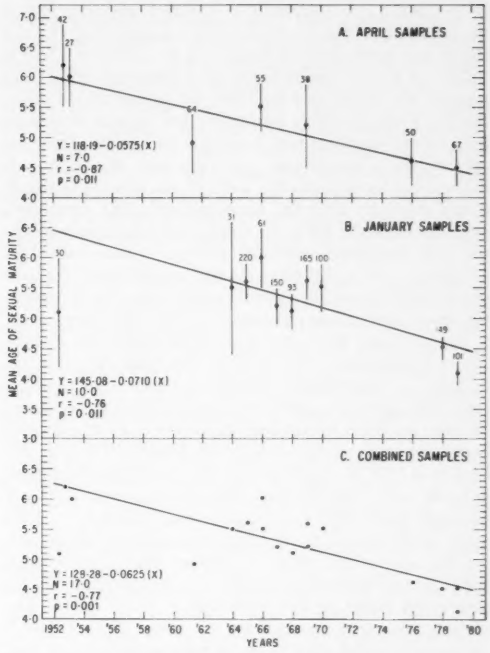

FIG. 1. Mean age of sexual maturity of female harp seals plotted against time for April (A), January (B), and combined (C) samples. Vertical lines indicate 95% confidence intervals of the mean. Numbers represent the number of females in the sample which contributed information to the calculation of the mean (see text).

TABLE 3. Mean age of sexual maturity ($\bar{x}$) of female harp seals, variance (S^2) of $\bar{x}$, and 95% C.I. of $\bar{x}$ for samples collected over the period 1951–79.

Year	Mean age sexual maturity ($\bar{x}$)	S^2 ($\bar{x}$)	95% C.I. of $\bar{x}$ Lower	Upper
	January–February samples			
1951–54	5.1	0.23	4.2	6.0
1964	5.5	0.30	4.4	6.6
1965	5.6	0.02	5.3	5.9
1966	6.0	0.07	5.5	6.5
1967	5.2	0.02	4.9	5.5
1968	5.1	0.03	4.8	5.4
1969	5.6	0.03	5.3	5.9
1970	5.5	0.05	5.1	5.9
1978	4.5	0.01	4.3	4.7
1979	4.1	0.03	3.8	4.4
	March–April samples			
1953	6.2	0.12	5.5	6.9
1952–54	6.0	0.07	5.5	6.5
1961–62	4.9	0.07	4.4	5.4
1966	5.5	0.05	5.1	5.9
1968–70	5.2	0.12	4.5	5.9
1976	4.6	0.04	4.2	5.0
1979	4.5	0.02	4.2	4.8

($P = 0.0003$; $r = -0.768$, $P = < 0.001$) explains 59% of the variability in mean age of sexual maturity (Fig. 1C) and shows that MAM declined from ~6.2 yr in 1952 to 4.5 yr in 1979 (see Table 3 for estimates of variance and 95% CI of means). We believe that the 1951–54 January MAM calculated by Fisher (1954) is particularly low because there were only six individuals of ages 5 and 6 in the sample. These are critical ages in determining age of maturity; thus an error in determining the reproductive status or age of a single female would markedly alter the mean estimate. The uncertainty associated with the 1951–54 January estimate is reflected by the wide confidence intervals (although underestimated by DeMaster's (1978) algorithm at small sample sizes). We have nevertheless retained this sample in the regressions as weighting makes appropriate compensation for sample size.

To investigate the relationship between mean age at maturity and population size, we regressed mean age of sexual maturity, as determined from January and April samples, separately against 1+ population size lagged 5 yr, using two different estimates of population size derived from sequential population analysis (Lett et al. 1978; Winters 1978 (Fig. 2)). Lett et al. (1978) suggested that the strongest correlations between mean age of sexual maturity and population size occurred when the 1+ population was lagged 5 yr. Both analyses of trends of 1+ population size gave similar results, but the regressions based on Winters (1978) consistently produced higher levels of significance. We present only the regressions based on data from Lett et al. (1978) for simplicity. We found a significant regression ($P = 0.015$) of mean age of sexual maturity on 1+ population size (Lett et al. 1979)) lagged 5 yr for April samples only, given by

$$(6) \quad \text{MAM} = 3.72 + 0.80\,(1 + \text{POP}_{t-5})$$

which explains 72.8% of the variation in mean age of sexual maturity (Fig. 3A).

We then increased the number of years lagged to 8 and found that the regression improves with an increasing lag (Table 4). Our analyses suggest that a lag of 8 yr is a much better predictor ($R^2 = 0.444$) of mean age of maturity than one of 5 yr ($R^2 = 0.285$).

Ovulation and Fertility Rates

Ovulation rates calculated from April samples of molting females are given in Table 2. There is no relationship between ovulation rate and 1+ population size. Mean ovulation rate during the period 1951–79 was 98.5%.

Fertility rates were estimated from January to February samples of southward migrating females captured in nets along the north shore of the Gulf of St. Lawrence and near St. Anthony, Newfoundland (Table 1). The 1964 estimate (81.8%) from Sergeant (1966) was omitted from the analysis for two reasons. First, the estimate was based on a small sample ($n = 33$ mature females). Second, a larger sample ($n = 104$) taken by Øristland (1971) in March 1964 on the Front provided a back-calculated estimate of 91.2%. Since the 1965 estimate of 92.6% is also based on a large sample ($n = 161$ mature females), it is more likely that the fertility rate in 1964 was closer to 91.2 than 81.8%.

We found a significant regression ($P = 0.012$; $r = 0.725$, $P = 0.012$; $R^2 = 0.526$) of fertility rate on time, given by the equation:

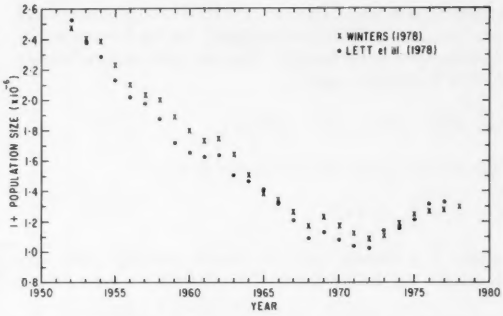

FIG. 2. Changes in 1+ population size over the period 1952–78 from Lett et al. (1978) and Winters (1978).

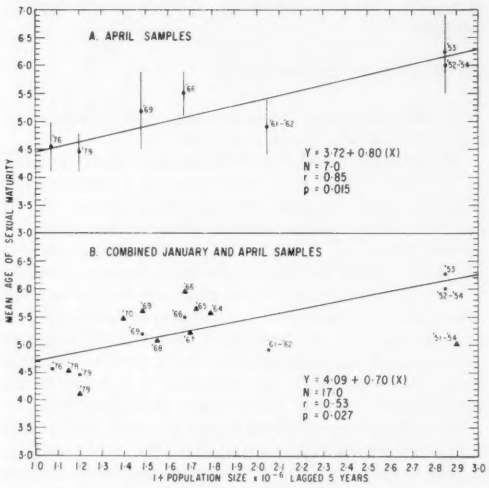
A. APRIL SAMPLES
Y = 3·72 + 0·80 (X)
N = 7·0
r = 0·85
p = 0·015
B. COMBINED JANUARY AND APRIL SAMPLES
Y = 4·09 + 0·70 (X)
N = 17·0
r = 0·53
p = 0·027
MEAN AGE OF SEXUAL MATURITY
1+ POPULATION SIZE x 10⁻⁶ LAGGED 5 YEARS

FIG. 3. Mean age of sexual maturity regressed against 1+ population size lagged 5 yr for April (A) and combined April and January (B) samples with 1+ populations from Lett et al. (1978) and Winters (1978).

$$(7) \quad y = 0.436(x) - 763.14$$

where x = year, for the period 1952–79. Fertility rate rose significantly over this period from 85% in the early 1950s to ~94% in recent years (Fig. 4).

Lett and Benjaminsen (1977) suggested plotting 2+ population size against fertility rate since younger animals remain segregated from the herd and thus would not compete with mature females. To test this we ran a series of weighted linear regressions of fertility rate on 1+, 2+, 3+, 4+, 5+, and 6+ population size in the previous year and obtained six highly significant ($P \leq 0.001$) regression equations explaining 74–75% of the variability in the pregnancy data (Table 5).

TABLE 4. Relationship between mean age of sexual maturity and 1+ population size lagged from 1 to 8 yr. $*P \leq 0.05$; $**P \leq 0.01$.

X	Slope	Intercept	r	Mult. R^2
1+ POP_{t-1}	0.3269	4.73	0.196	0.038
1+ POP_{t-2}	0.4778	4.50	0.293	0.086
1+ POP_{t-3}	0.6444	4.22	0.418	0.175
1+ POP_{t-4}	0.7142	4.11	0.526*	0.277
1+ POP_{t-5}	0.7012	4.09	0.534*	0.285
1+ POP_{t-6}	0.7124	4.05	0.588*	0.345
1+ POP_{t-7}	0.7228	4.00	0.655**	0.430
1+ POP_{t-8}	0.6930	4.00	0.677**	0.444

We chose a 1-yr lag because it seemed likely that population density at the time of ovulation and subsequent implantation might significantly affect fertility. The regressions of fertility rate on time and population size were repeated using the arcsin transformation of the fertility data (Snedecor and Cochran 1967). With time as the independent variable, significances were lower ($P \leq 0.04$) and the regressions explained only 39% of variability in fertility rate. Similar reductions in significance ($P \leq 0.01$) and variability explained by the regressions (58–60%) were observed with population size as the independent variable (Table 5). In all cases normality plots of the residuals showed that the arcsin transformation made the data less, rather than more, normal. We concluded that this transformation served no useful purpose when applied to these data.

Discussion

Age of Maturity

The regressions of mean age of sexual maturity against year were significant when winter and spring samples were treated separately and highly significant when the samples were combined. Our analysis shows that the mean age of sexual maturity declined during the period (1952–1979) covered by the biological data.

Several authors have concluded that mean age of sexual maturity of female harp seals is density-dependent (Winters 1978; Lett et al. 1978; Lett and Benjaminsen 1977; Sergeant 1973, 1976). Using the estimates of population size derived by Lett et al. (1978) and Winters (1978), we have shown significant relationships between mean age of sexual maturity and 1+ population size lagged anything from 4 to 8 yr, with the 8-yr lag showing the highest significance level. Little difference was found between the relationships based on the two population estimates, and what little there was can probably be explained by differences in the methods used by Lett et al. (1978) and Winters (1978).

However, the results reported here should be interpreted with caution, for a number of reasons. Firstly, we were unable to demonstrate a significant relationship between the mean age of maturity calculated from winter samples and population size. On the other hand, the combined winter and spring data yielded significant regressions using population estimates of both Winters (1978) ($r = 0.59$, $P = 0.012$) and Lett et al. (1978) ($r = 0.53$, $P = 0.027$). Secondly, the analyses of Winters (1978) and Lett et al. (1978) only estimated population size back to 1952. Thus it was necessary to extrapolate beyond the data to lag the early 1950s samples more than 2 yr. We used a linear extrapolation of the population trend based on the two cohort analyses (Lett et al. 1978; Winters 1978). Finally, because the temporal trend is nearly linear for population size, and appears roughly so for mean age of maturity against time, it is extremely difficult to determine statistically the appropriate lag factor from the data alone. On biological grounds, a lag of 5 or 6 yr is reasonable as these age-groups generally contribute the most to the estimation of mean age at maturity (large values of $P(x)$ in equation 3)).

Sergeant (1973) proposed that the decrease in mean age at maturity was brought about by an increase in growth rate as population size declined. Innes et al. (1980) reported evidence that the growth rate of young harp seals sampled in the 1970s is higher than that of animals sampled in the 1950s. However, they point out that the conclusion of density-dependent growth must remain tentative as the 1950s data are not totally comparable with recent information.

Harp seals sampled in the 1950s reached maturity at 92.3% of final body length (Laws 1956) at an average age of 6.2 yr (this study). Current data indicate that harp seals now reach maturity at 90.8% of final body length (Innes et al. 1980) at a mean age of 4.5 yr (this study). Sexual maturity in most Phocidae is attained at a rather constant proportion of adult body length and is reached earlier when growth is accelerated (Laws 1956, 1959). Thus, if other conditions remain constant, a reduction in population size may lessen competition for food, increase per capita food availability, lead to increased growth rates and earlier maturation of young animals.

Ovulation and Fertility Rates

Confusion regarding the density-dependent nature of fertility rates of harp seals appears to have occurred for two reasons. Sergeant (1966, 1978) concluded that there had been no change in the fertility rate of older females (age 8+) from 1951 to the present. In fact, this is true. However, the true population fertility rate should include all mature females regardless of age. When this is done, it is clear that fertility rate has increased (Fig. 4). The second source of confusion arose out of the indiscriminate combination of ovulation and fertility rates and the use of an incomplete data set by Lett et al. (1978). This resulted in a fortuitous relationship between fertility rate and population size. The conclusion of Winters (1978: 1258, fig. 7) that there is no relationship between fertility rate and population size is also in error.

Regressions of fertility rate on 1+, 2+, 3+, 4+, 5+, and 6+ population size were all highly significant. The question then arises as to which of the six regressions (1+, 2+, etc.) is the most appropriate. There is evidence that young-of-the-year behave differently from the rest of the herd (Sergeant 1976). They tend to remain separate from older animals and to form a larger percentage of the summer population off West Greenalnd (Sergeant 1965, 1976; Kapel 1975, 1978), becoming more closely integrated with the remainder of the herd as they grow older. So there is some basis for excluding the young-of-the-year from the population that influences

TABLE 5. Relationship between fertility rate (%) and 1+, 2+, 3+, 4+, 5+, and 6+ population size in previous year. $^{**}P \leq 0.01$; $^{***}P \leq 0.001$. [a]arcsin transformation on percentages.

	Raw pregnancy data				Transformed[a] pregnancy data		
X	Slope	Intercept	r	Mult. R^2	Slope	r	Mult. R^2
1+ POP_{t-1}	−7.977	105.33	-0.864^{***}	0.747	−0.146	-0.770^{**}	0.594
2+ POP_{t-1}	−8.488	104.81	-0.862^{***}	0.742	−0.154	-0.763^{**}	0.583
3+ POP_{t-1}	−9.704	104.99	-0.862^{***}	0.743	−0.176	-0.763^{**}	0.583
4+ POP_{t-1}	−11.391	105.35	-0.861^{***}	0.742	−0.207	-0.763^{**}	0.583
5+ POP_{t-1}	−12.220	104.72	-0.858^{***}	0.736	−0.222	-0.759^{**}	0.577
6+ POP_{t-1}	−12.590	103.58	-0.870^{***}	0.756	−0.230	-0.777^{**}	0.603

pregnancy rates in females, which do not become sexually mature before the age of 3 yr.

Similar reasoning could be used to argue that 1-yr-old animals will have less influence on the sexually mature females than 2-yr-old animals. Such an argument is only weakly supported by the data; there is no practical way to distinguish statistically significant differences in the series of correlation coefficients. Thus, although Lett and Benjaminsen (1977) suggested plotting 2+ population size against fertility rate, we can see no basis for excluding 1-yr-old animals from the analysis.

The proposed density-dependent changes in mean age of sexual maturity and fertility rate rely heavily on the meager data from the early 1950s. This is unfortunate for, as Rivard (1978) has pointed out, our understanding of these relationships is unlikely to improve substantially until population size has once again reached a high level. Under a management policy ensuring a 5% annual increase in the 2+ population, this would not occur until the 1990−99 period, but given our present knowledge of the population (Winters 1978), a 5% increase would seem overly optimistic. Rivard's (1978) analysis clearly indicates that additional collections of reproductive samples in the near future will not reduce substantially the uncertainties associated with these possible density-dependent relationships.

Although direct evidence of density dependence in reproductive parameters is yet forthcoming, data from the White Sea harp seal population are consistent with a density-dependent response. The White Sea population declined from an estimated 3 million 1+ animals in 1928 to 600−700 thousand animals in 1939 (Dorofeev and Freiman 1928; Yakovenko 1963). During the war years the population recovered, reaching an estimated 1.25−1.50 million by the early 1950s (Surkov 1957). However, by the early 1960s the population had been reduced to 455 000. Management actions taken at this time have reportedly allowed the population to increase to about 800 000 animals in 1978 (Benjaminsen 1979). This 1978 population estimate is based on a forward projection of the 1965 pup production using the rates of fertility and natural mortality estimated from the Northwest Atlantic harp seal population. If the rate of natural mortality for the White Sea population is in fact higher, the estimated 1978 population size would be lower.

Reproductive samples were collected by Nazarenko (1975) from 1962 to 1964 and in 1969 and 1971. His data showed that median age of sexual maturity fell from 4.6 in 1962 to 4.0 and 4.1 in 1963 and 1964. Subsequently, median age of sexual maturity increased to 4.8 yrs in 1969 and 1971. Thus

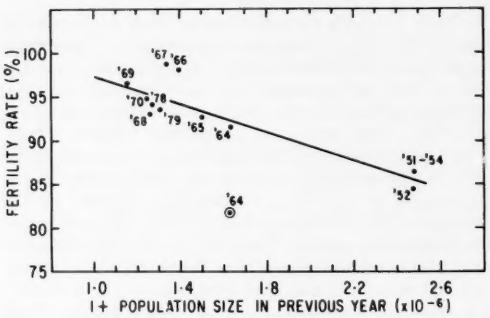

FIG. 4. Fertility rate regressed against 1+ population size in the previous year. The circled 1964 point was eliminated from the analysis, see text.

median age of sexual maturity has changed with corresponding changes in population size. The rather rapid rate of recent increase in median age of maturity is surprising. This means that this parameter may provide a useful indicator of population change which is probably as sensitive as that provided by aerial census or mark−recapture techniques. However, although the population of Northwest Atlantic harp seals is thought to have increased slightly since the early 1970s (Lett et al. 1978; Winters 1978), no increase in mean age at maturity has been observed (Table 3).

From the point of view of population dynamics, mean age of maturity is not as useful as age-specific reproductive rates. These, in combination with age-specific survival rates, govern the rate of population change. However, mean age of maturity is a convenient index of change in the reproductive potential of a species. Consequently, continued study of harp seal reproduction and in particular the mechanisms responsible for changes in reproductive parameters will play an important role in the management of this species.

Acknowledgments

We thank Drs D. Roff, K. Hay, and D. M. Lavigne and an anonymous referee for critically reviewing the manuscript.

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Seasonal Particle-Size Selection by *Diaptomus sicilis* in Offshore Lake Michigan[1]

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VANDERPLOEG, H. A. 1981. Seasonal particle-size selection by *Diaptomus sicilis* in offshore Lake Michigan. Can. J. Fish. Aquat. Sci. 38: 504–517.

Diaptomus sicilis feeding on offshore Lake Michigan seston exhibited a relatively invariant pattern of particle-size selection in 23 separate feeding experiments conducted from spring through fall over a 2-yr period. This pattern persisted for different feeding rates under varying conditions of particle-size spectrum shape, abundance and food quality of particles, and temperature. Selection was quantified by calculating W' (filtering efficiency) as a function of particle size (equivalent spherical diameter). In all but one of the few experiments yielding a W' curve that varied appreciably from the other W' curves, serious bias from grazer-produced particles was evident and/or elongated particles dominated the seston. The elongated particles could have led to deviations because of differences in filtering efficiency between round and elongated particles of small volume and because elongated particles of large volume have to be captured raptorially. It is argued that the more variable patterns of particle-size selection observed in many of the other studies of zooplankton feeding on natural seston result from: (1) improper methods of quantifying selection, (2) serious bias from grazer-produced particles, and (3) varying particle shape, which is not usually specified. The mechanisms of particle selection by *Diaptomus* and other species that filter like *Diaptomus* are reviewed, and it is noted that invariant selection is not inconsistent with both filtering and raptorial modes of feeding operating simultaneously. All the evidence points to a strong passive-mechanical filtering mode of feeding that may be supplemented by a raptorial mode of feeding that selects large particles of high food quality.

Key words: Diaptomus sicilis, particle-size selection, filter feeding, peak tracking, passive selection, Lake Michigan, food selectivity

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Au cours de 23 essais séparés d'alimentation menés du printemps à l'automne inclusivement sur une période de 2 ans, *Diaptomus sicilis* se nourrissant de seston du lac Michigan exerçait une sélection relativement invariable de grosseur de particules. Les modalités de cette sélection persistèrent avec divers taux d'alimentation dans des conditions variables de grosseur et de forme de particules, abondance et qualité nutritive et enfin température. Nous avons quantifié la sélection en calculant W' (efficacité de filtrage) comme fonction de la grosseur des particules (diamètre sphérique équivalent). Dans tous les rares essais, sauf un, qui donnèrent une courbe W' différant de façon appréciable des autres, on a pu constater un biais important causé par des particules produites par les brouteurs et (ou) la prédominance de particules allongées dans le seston. Ces dernières pourraient occasionner des déviations par suite de différences d'efficacité de filtrage entre particules rondes et particules allongées et aussi par suite du fait que les particules allongées de gros volume doivent être saisies. Nous arguons que les modalités plus variables de la sélection de la grosseur des particules observées dans plusieurs autres études sur du zooplancton se nourrissant de seston naturel sont dues à: (1) des méthodes inappropriées de quantification de la sélection, (2) un biais important résultant de particules produites par les brouteurs et (3) une variation de la forme des particules, qui n'est ordinairement pas spécifiée. Nous passons en revue les mécanismes de sélection des particules par *Diaptomus* et autres espèces qui filtrent de la même manière, et nous notons que le peu de variation dans la sélection s'applique à la fois au filtrage et à la capture, fonctionnant simultanément, comme méthodes d'alimentation. On a de fortes indications qu'il s'agit d'un mode de filtrage mécanique passif bien implanté, auquel peut s'ajouter

[1]GLERL contribution No. 247.

Printed in Canada (J6149)
Imprimé au Canada (J6149)

un mode d'alimentation par capture, selon lequel de grosses particules de haute qualité nutritive sont sélectionnées.

Received July 9, 1980
Accepted January 27, 1981

Reçu le 9 juillet 1980
Accepté le 27 janvier 1981

DIAPTOMID copepods (Suborder Calanoida) are very abundant in all the Laurentian Great Lakes and so are responsible for a large fraction of the grazing there. *Diaptomus sicilis*, an obligate herbivore (Warren unpublished data) found in all the Great Lakes (Robertson 1966), is an important component of the zooplankton in offshore Lake Michigan. The ultimate goal of this research is a feeding construct that will predict the amounts of different kinds of phytoplankton and other seston that *D. sicilis* will eat at various concentrations of different kinds of seston found in lake water. Such information is required for realistic simulation of both phytoplankton and zooplankton dynamics. Some experimenters have argued that food selection by calanoid copepods is passive and mechanical, a function of the pore-size distribution of the copepod's filter and its ability to handle and ingest particles of various sizes (Nival and Nival 1973, 1976; Boyd 1976; Frost 1977). Passive, mechanical selection implies that particle selection can be expressed on the basis of size by time-invariant selectivity coefficients (W_i') that are mathematically equivalent to filtering efficiencies (Vanderploeg and Scavia 1979a). The question of whether food selection can be expressed by simple time-invariant coefficients is important because invariant coefficients greatly simplify the problem of predicting the amounts of different kinds of food eaten (Vanderploeg and Scavia 1979a).

Support for the concept of passive, mechanical selection in marine calanoid copepods comes from the laboratory feeding experiments by Frost (1977) on *Calanus* and from arguments of Boyd (1976) and Frost (1977) based on morphology of feeding appendages (Marshall 1973; Nival and Nival 1973, 1976) and results of earlier published work on feeding of copepods in mixtures of cultured species of phytoplankton (Marshall and Orr 1955; Mullin 1963). On the other hand, Poulet (1973, 1974, 1978) from studying *Pseudocalanus*, Richman et al. (1977) from studying *Acartia* and *Eurytemora*, Cowles (1979) from studying *Calanus*, *Eucalanus*, and *Centropages*, and Richman et al. (1980) from studying *Diaptomus* all concluded that feeding on natural particle-size spectra is not passive and mechanical, but that copepods preferentially select, or track, peaks of abundance in natural particle-size spectra. Recent laboratory experiments (Poulet and Marsot 1978; Donaghay and Small 1979; Donaghay 1980) demonstrated that *Acartia*, which uses its filter (second maxillae) in a seining motion to capture particles, has a complicated behavorial repertoire that can radically modify the filtering behavior expected from the morphology of its filter. *Acartia* can definitely reject particles it has captured on its filter, and this behavior is dependent on food taste and preconditioning of *Acartia* to different foods. Donaghay (1980) notes that his own observations indicate that *Eurytemora*, which sets up currents of water through a fixed filter (second maxillae) like *Calanus*, has many of the behavioral capabilities of *Acartia*, whereas *Calanus* does not. The differing behavior of *Eurytemora* and *Calanus* may be related to behavioral and sensory adaptations associated with the strongly omnivorous nature of *Eurytemora* (Lowndes 1935). The laboratory observations on feeding of *Calanus* and similarity in filtering mechanisms among *Calanus*, the diaptomid copepods, and *Pseudocalanus* (Easterly 1916; Cannon 1928; Lowndes 1935; Gauld 1966; Strickler and Rosenberg unpublished data) would suggest that this group of genera should have a strong passive-mechanical component of food selection. This group of copepods will be hereafter called "*Calanus*-like" copepods. Thus, the peak tracking by *Calanus*-like copepods in natural seston runs counter to the passive-mechanical selection observed in laboratory experiments.

As my first step taken to understand grazing by *D. sicilis*, I used a Coulter counter to measure its size-selective grazing during different seasons in the offshore region of the southern basin of Lake Michigan. This oligotrophic–mesotrophic region exhibits a classic pattern of seasonal succession of algae proceeding from diatoms to green and blue-green algae, with green and blue-green algae becoming significant during late summer and fall (Tarapchak and Stoermer 1976). Thus, by studying particle-size selection in different seasons, I would be studying selection under conditions of varying algal composition and, presumably, of varying food quality (Arnold 1971; Porter 1977).

Specifically, I hypothesized at the initiation of this study that food-size selection by *D. sicilis* in nature is strongly passive and mechanical. In this paper, I will show that the pattern of food-size selection by *D. sicilis* is relatively invariant from experiment to experiment and from season to season. These and other results support the hypothesis that food-size selection by *D. sicilis* has a strong passive-mechanical component. Moreover, I argue that the more variable patterns of food-size selection and peak tracking observed in many studies of copepod grazing on natural seston are caused by particle shape, are artifacts of methods of quantifying results, or are artifacts resulting from serious interference from particles produced by the copepods while feeding.

Methods

Zooplankton and lake water were collected between dawn and mid-morning at an 80-m-deep station 15 km west of Grand Haven, MI. Zooplankton were collected with a WP-2 opening–closing net (Fraser 1968) of 200-μm mesh. During seasons when the lake was isothermal, water for experiments came from a depth of 4 m, and zooplankton were collected in vertical tows from the lake bottom or mid-depth to the surface. When the lake was thermally stratified, water was collected from the lower metalimnion or upper hypolimnion, regions where *D. sicilis* are found at night and often during the day (Patalas 1969; Wilson and Roff 1973; M. Evans, Great Lakes Research Division, Univ. of Michigan, Ann Arbor, MI, 1979, personal communication); zooplankton were collected in vertical tows through the hypolimnion. Upon collec-

tion, water was placed in insulated 11-L plastic-lined jugs (Coleman Co.). Some of the jugs were used for transporting lake water and others were used to transport zooplankton. The jugs of zooplankton and water arrived at the laboratory from 1 to 8 h after collection, during which period the water temperature did not usually change by more than ±3°C. Upon arrival, the jugs were placed in an incubator to restore them to original lake temperature.

Experiments were set up on the same days, usually late in the evenings, that water and zooplankton were collected. Water to be used for experiments was gently screened with a 153-μm screen to remove larger zooplankton. Stage VI *D. sicilis* females were sorted using an eyedropper. Actively swimming, apparently uninjured stage VI females were washed with several millilitres of 153-μm-screened lake water, recaptured with the eyedropper, and placed in a prefeeding beaker, a 250-mL beaker filled with 153-μm-screened lake water maintained at lake temperature. To prevent possible addition of extraneous particles to experimental containers, in most cases I used only females not carrying egg sacs or spermatophores. For each experiment there were two control bottles (without zooplankton) and one or two experimental bottles (with zooplankton) of 275-mL or 300-mL volume.

To keep seston in suspension and limit algal growth, the control and experimental bottles were placed on a rotating wheel at 0.25 rev min^{-1} in the dark in an incubator set to lake temperature (McQueen 1970). Generally, dark limitation of algal growth started several hours before placing bottles on the wheel because the lake water was usually kept in the dark most of the time after collection. After 0.8–1.1 d of incubation, the bottles were removed from the wheel and their contents poured through a 200-μm or 250-μm screen to remove the zooplankton. All bottles were poured through the screen to assure that all bottles received the same handling.

Three series of experiments warrant special note because they differ somewhat from the general design. Lake water in experiments of September 13–14, 1977, and October 25–26, 1977, was diluted with 0.2-μm-filtered lake water to ensure that the number of *D. sicilis* obtained would graze down a significant fraction of the seston during this period. I had found that filtering rates for this and other species of *Diaptomus* were low at this time. Borrowing the experimental design of Richman et al. (1977), I carried out a series of three experiments on July 25–26, 1978, with the same water, but a different number of zooplankton in each of the experiments. This series was done to test if the W' vs. particle-size curve changes as larger and larger fractions of differently sized food are removed. Lastly, a series of four experiments during November 7–11, 1977, was designed to determine if experiments on water and zooplankton that were shipped (by car or air freight) from the field laboratory in Grand Haven to the laboratory in Ann Arbor, MI, and held 1 d before use in an incubator would give results different from those obtained with freshly caught zooplankton and lake water.

In this last series of experiments, two sets, a "fresh" set and a "1-d-old" set, of jugs of zooplankton and water were collected on the 1st day of the experiments at about 09:00 EST. Upon arrival at the field laboratory in Grand Haven at about 10:30 EST, the fresh set of jugs of zooplankton and water was placed with tops removed in an incubator set to the lake temperature and to the local photoperiod at a light intensity of ~2000 lx. The 1-d-old set was left outside with the tops still on until ~17:00 to simulate travel from Grand Haven to Ann Arbor. After that period, it was placed, like the other set, in the incubator. Temperature increase in these jugs was less than 2°C. A feeding experiment with the fresh zooplankton and water was set up by about 15:00. An experiment with the 1-d-old set of water and zooplankton was set up about 24 h later. On the 3rd day, water was collected again, and these two experiments were repeated.

A TA II Coulter counter was used in conjunction with the basic method devised by Sheldon and Parsons (1967) to obtain particle-size spectra (both number and volume concentration). To acquire a continuous particle-size spectrum over the range of particle sizes grazed by *D. sicilis*, I used the following combinations of aperture tubes: 50 and 200 μm; 50, 140, and 400 μm; and 140 and 400 μm. Starting in summer 1977, settled samples of preserved, 153-μm-screened lake water from the same jug from which the experimental water came were examined on the inverted microscope before Coulter analysis to determine the presence or absence of long fiber-shaped particles. The largest Coulter counter aperture tube was selected so that the aperture width was as great or greater than the length of the longest common alga in the sample.

Lake water was made conductive by adding enough 0.2-μm-filtered 25% NaCl solution to make a 0.5% solution of NaCl. After adding salt, samples were stirred for at least 4 min to allow air bubbles, which could be counted by the Coulter counter, to escape from suspension. Subsamples of water from all the bottles were run in quadruplicate on the largest aperture tube before moving on to the next largest aperture. Samples were diluted just before analysis, if necessary, with 0.2 μm-filtered lake water to bring coincidence (as monitored by the concentration index meter of the TA II Coulter counter) below 1.5% for all aperture tubes.

The filtering rate on each size category was calculated for each experimental bottle from the Richman et al. (1977) modification of Gauld's (1951) equation. For control concentration (counts · mL^{-1}) required in this equation, I used mean concentration of the two control bottles. When two experimental bottles were used, a mean filtering rate was calculated from the separate filtering rates determined for each bottle.

In some cases, concentration in certain size categories was higher in experimental bottles than in control bottles, resulting in negative filtering rates. Since zooplankton cannot filter at negative rates, negative filtering rates were assigned zero values (Richman et al. 1977; Vanderploeg and Scavia 1979a). Particle production by zooplankton during feeding (Frost 1977; Richman et al. 1977; Vanderploeg and Scavia 1979a) is a major cause of negative filtering rates (Richman et al. 1977; Vanderploeg and Scavia 1979a).

The selectivity coefficient W' was calculated by dividing the filtering rate of a size category by the largest filtering rate (F_{max}) observed in any of the size categories (Vanderploeg and Scavia 1979a). When W' is estimated from filtering rates, this estimate is unaffected by the amount of food eaten in an experiment, even though the individual filtering rates may vary over time (Vanderploeg and Scavia 1979a, b). On the

assumption that a copepod can be treated as a filter feeder, F_{max} is the pumping rate of water through the filter, and W' is the filtering efficiency (Vanderploeg and Scavia 1979a). The selectivity coefficient W', which was derived from simple concepts of probability theory as a general tool for studying predator–prey interactions, is mathematically identical with retention (filtering) efficiency as used by certain zooplankton ecologists (Harbison and McAlister 1979; Nival and Nival 1979; Runge 1980).

Two feeding rate quantities were calculated. The first, called net feeding rate in the jth experimental container, is equivalent to Poulet's (1973, 1974) food consumption. It was calculated from the sum over all size categories of the differences between mean concentration of particulate material in the control containers and concentration in the jth experimental container

$$\mathrm{NFR}_j = (V/tN_j)\sum_i(\bar{C}_i - Z_{ji}),$$

where NFR_j = net feeding rate (NFR) in jth experimental container ($10^6\mu m^3 \cdot animal^{-1} \cdot d^{-1}$), V = volume of bottles used in the experiment (mL), t = time duration of the experiment (d), N_j = number of zooplankton in experimental container j (j = 1,2), $\bar{C}_i$ = mean concentration of particulate material in control containers in size category i ($10^6\mu m^3 \cdot mL^{-1}$) and Z_{ji} = concentration of particulate material in experimental container j in size category i ($10^6\ \mu m^3 \cdot mL^{-1}$). The second quality, called gross feeding rate (GFR) in the jth experimental container (GFR_j), was calculated in the same way as NFR_j, except that only positive differences, $\bar{C}_i - Z_{ji}$, were summed. As with the case of filtering rates, a mean *NFR* and a mean *GFR* were calculated from the separate NFR_js and GFR_js. If GFR is much larger than NFR, particle production by zooplankton while feeding was significant, and one or both measures of feeding rate are poor estimators of ingestion. Concentration of particulate material found in the control containers at the end of the experiment and NFR and GFR are strictly correct measures of food supply and feeding only if the concentration of particulate material does not change in the control container over the period of the experiment. A given relative change in concentration in the control container results in the same relative change in estimates of NFR and GFR. Since concentration in most size categories in the control containers, as revealed by measurement of initial control concentration for some experiments, usually decreased over the period of the experiment by ~10%, the estimates of food concentration, NFR, and GFR will be slightly lower than true values. This slight bias will not have a significant effect on any conclusions drawn. The ratio NFR/GFR that is used extensively in the analyses of particle production below is free of this bias.

Number concentration (counts $\cdot$ mL^{-1}) of individual particles in sea (Sheldon and Parsons 1967; Poulet 1973, 1974) and lake water is roughly inversely proportional to particle volume. As a result, fewer particles are counted by the Coulter counter in larger size categories. Counting follows Poisson statistics, which predict that the standard deviation of a count is equal to its square root. Thus, precision in concentration estimation decreases with increasing size of particles. A 25% counting error, which would occur with a count of 16, was determined to be unacceptable for calculation of meaningful filtering rates and W's because a 25% removal of food from a size category represented a filtering rate that was a significant fraction of the largest filtering rate observed for any size category. Using the total counts sampled by the Coulter counter for both controls for each size channel, I chose the first channel where the total counts recorded in the controls were less than 16 as the cutoff point for the case of two experimental containers. For the case of one experimental container, the cutoff point total was 32. As expected, percent standard errors on filtering rates calculated from the separate filtering rates generally become quite large in size categories beyond the cutoff point.

During both 1977 and 1978, 100 mL of water pooled from both control containers was preserved with Lugol solution (1%) for later identification on slides of oil-cleared membrane filters (Moore 1963). Slides were made for the 1977 samples, but not for the 1978 samples. During 1978, I became interested in knowing the contribution of fecal material to the measured particle-size spectra in experimental containers. In addition, my own experimental work (unpublished) and the other work in our laboratory (Eadie unpublished data) had shown that $CaCO_3$ crystals were an important component of the seston during late summer.

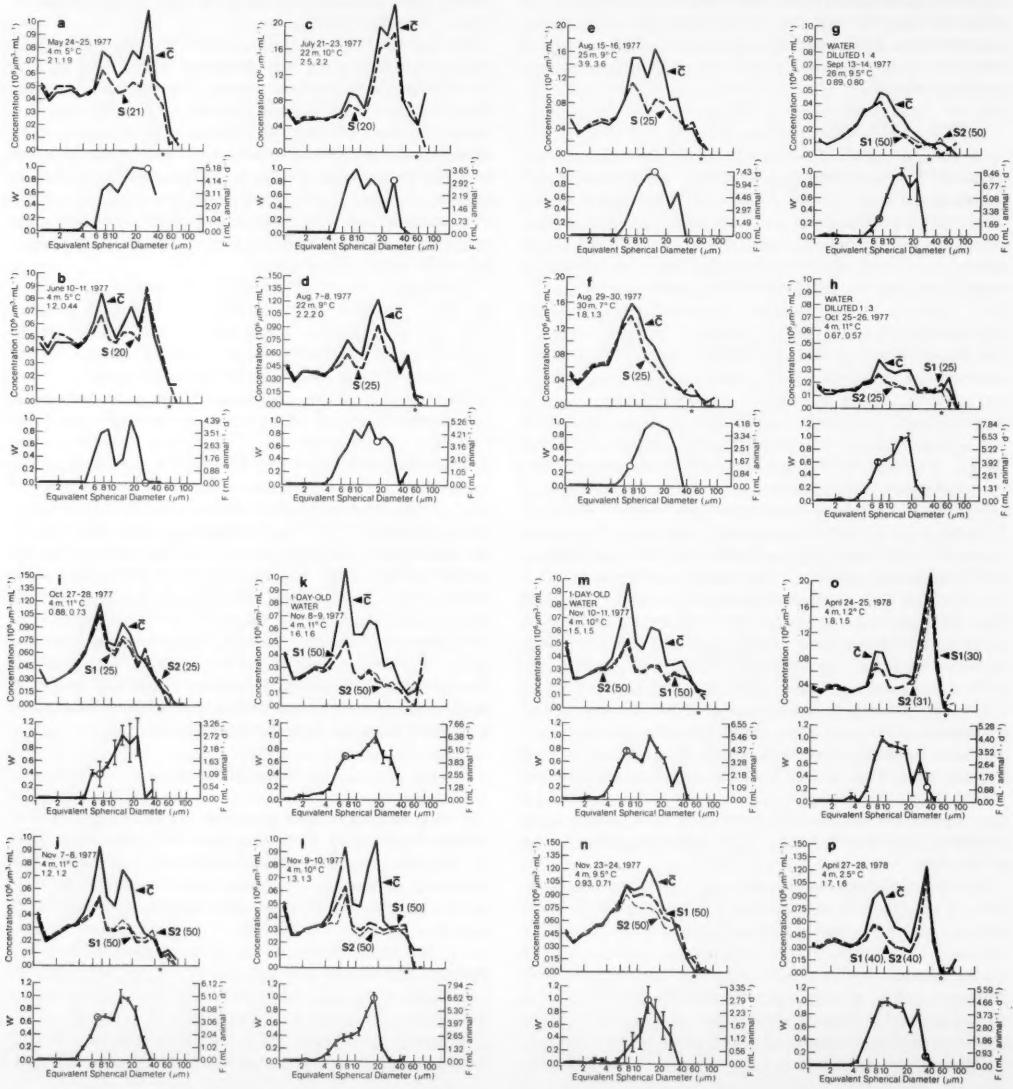
To obtain a visual record of fecal material and $CaCO_3$ crystals, I used the following methods. In all the analyses described above for the Coulter counter, a 90-mL or 180-mL subsample of water was poured into a beaker for analysis with the largest aperture tube selected for an experiment. After Coulter analysis, usually more than 50 mL of the subsample remained in the beaker. This water was preserved with filtered formalin (1%), immediately filtered through a membrane filter, washed with 30 mL of a filtered 1% solution of formalin in lake water to remove the salt, and cleared with oil for later microscopic examination (Moore 1963). This method allowed examination of fecal pellets remaining at the end of the experiment after exposure to salt and stirring on the Coulter sample stand. The oil cleared the peritrophic membranes of the fecal pellets, thus allowing viewing of their contents. $CaCO_3$ crystals were preserved by this method as well. Because of the low pH of the Lugol preserved samples (pH < 4), $CaCO_3$ crystals were lost in them. Thus in 1978, all observations of seston (in control containers) and fecal pellets (in experimental containers) were made on slides made from water left over from Coulter analyses.

Results

Two guiding principles motivated the design and analyses of these experiments. First, selectivity should be expressed by W'. By determing if the W' vs. particle-size curve changes for various experimental conditions, one can determine if the pattern of selection (filtering efficiency) is invariant. In the context of known mechanisms of copepod feeding (Frost 1977), the simplest explanation of an invariant W' pattern is passive, mechanical selection. If W' is not invariant, the hypothesis of passive, mechanical selection is contradicted. In addition, the behavioral phenomenon of peak tracking, or peak selection, implies that W' curves should have a shape similar to the curve for concentration of seston in the control

containers. Thus, the curves will be examined not only for their invariance, but also for their similarity to the curves for concentration of seston in the controls. Second, a moderate fraction of food must be removed from one or generally several size categories to quantify selection accurately. As already noted, counting errors can be quite large in larger size categories. Also, in small size categories, percent standard error of the mean of the controls was on the order of 1−5% for most experiments. These counting and replication errors can mask true patterns of food selection unless an appreciable fraction of the available food is eaten. Although the estimate of W' is unaffected by the fraction of food eaten in an experiment, this fraction should not be too great, or else potential correlations between W' and relative abundance of food in different size categories in the control containers would not be meaningful owing to gross changes in food concentration during the course of the experiment.

The results of the 23 separate feeding experiments are shown in chronological order in Fig. 1 (a−w). The upper graph of each part shows the concentration of seston in the control and in the experimental containers at the end of the experiment. Water depth, temperature, GFR, and NFR are



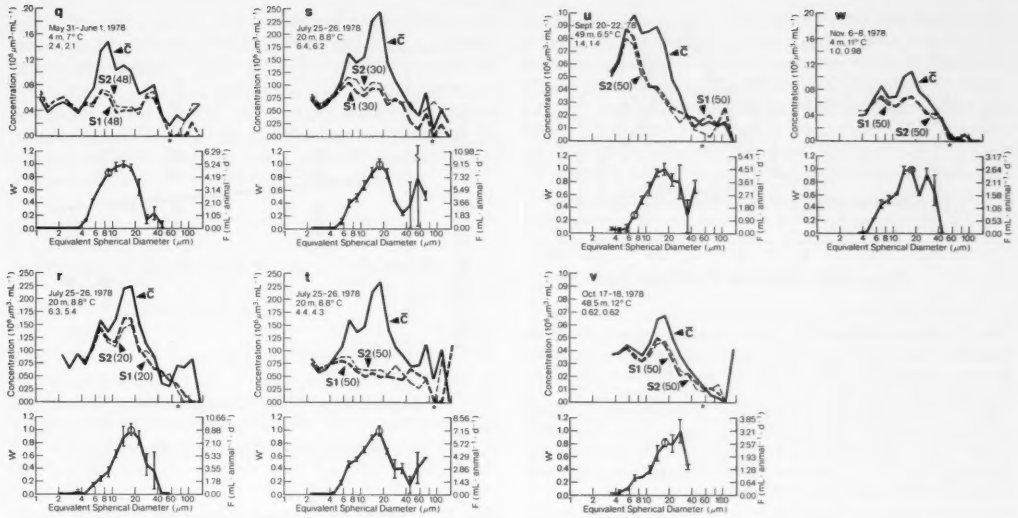


FIG. 1. Results of 23 (a−w) separate feeding experiments with *Diaptomus sicilis*. In the row below the date, depth and water temperature are given. The last row gives GFR and NFR. $\bar{C}$ is the mean concentration of seston in the control containers at the end of the experiment. S is the concentration in the experimental container, with the value in parentheses indicating the number of animals in the container. $S1$ and $S2$ designate experimental containers 1 and 2, if two were used. The asterisk on the abcissa of the concentration graph indicates the statistical cutoff point for calculation of W', F, and feeding rate. (See text.) A circle is drawn around the W' value in the size category of maximum $\bar{C}$.

also given. The lower portion shows W' and filtering rate (F) curves. In most experiments, a moderate amount (20−30%) of the food was eaten.

General Patterns of Selection

Invariance of W′ and peak tracking — A scan through the separate experiments in Fig. 1 shows that although a wide variety of particle spectra in control containers was available as food, most of the W' curves are quite similar. An overall mean W' curve calculated from all 23 of the separate experiments except the June 10−11, 1977, experiment (see below) is shown in Fig. 2. The mean W' curve is smooth and has moderate standard deviations. This reflects the roughly invariant pattern of particle-size selection exhibited in the different experiments. The overall mean curve can be used as a benchmark to compare with W' curves of separate experiments. Using it this way, we see that all except Fig. 1b and ℓ resemble the overall mean W' curve. Further, the W' curves bear little resemblance to the curves for particle concentration in the control containers. Thus, in general, a relatively invariant pattern of selection that is inconsistent with peak tracking was found.

Another way of looking at these results is to plot the size category of F_{max} as a function of the size category of maximum seston concentration in the controls (Fig. 3). A linear regression resulted in a slightly negative slope that was not significantly different from zero. Of particular interest is that F_{max} in 19 out of 23 cases was located in the 14- and 18-μm size categories, that is, within two adjacent size categories. The relatively invariant location of F_{max} and the slope of the regression again argue for an invariant pattern of selection and against peak tracking.

The experiments done to show the effect of extent of food removal (Fig. 1: r−t) on W' imply that, at least for size categories up to 40 μm, the amount of food removed has no appreciable affect on the W' curve. Because of the different number of zooplankton in the containers and correspondingly different quantities of food removed, the zooplankton in these experiments were exposed to different time histories of particle-size spectrum shape and magnitude.

W' curves were remarkably similar for *D. sicilis* exhibiting different values of feeding rate and F_{max} during different seasons and for varying concentrations of food. Table 1 shows that feeding rates (both NFR and GFR), filtering rates, and total quantity of particulate material ($\Sigma\bar{C}_i$) in the control containers (up to the statistical cutoff point) varied considerably among seasons. Mean values of feeding rates, F_{max}, and $\Sigma\bar{C}_i$ were all greatest in midsummer. During late summer and fall, when the temperature of the experiments was about the same as in midsummer, lowest average values of these variables were observed. When means of midsummer experiments are contrasted with means of all late summer and fall experiments (excluding those with diluted water; Table 1), differences between all means are significant at the 5% level. All these variables except F_{max} had intermediate values during spring.

Particle production — Particle production can result from: (1) breakup of delicate chain-forming algae during feeding (O'Connors et al. 1976), (2) sloppy chewing of individual

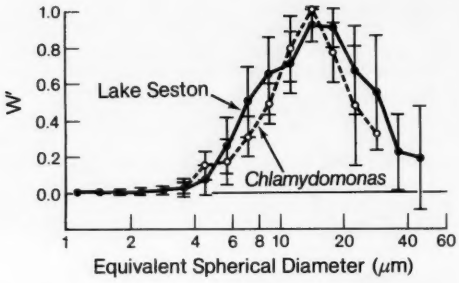


FIG. 2. The overall average W' curve for *Diaptomus sicilis* calculated from the results of the 23 separate experiments with lake seston for size categories up to 50 μm. Error bars represent ±1 SD for the population of observed W's. Number of observations for the size categories shown ranged between 14 and 22 owing to fewer observations on the smallest and largest size categories. Too few observations (three or less) were made on size categories >50 μm to present meaningful results. Also shown is the overall mean W' curve for four experiments with mixtures of *Chlamydomonas* spp.

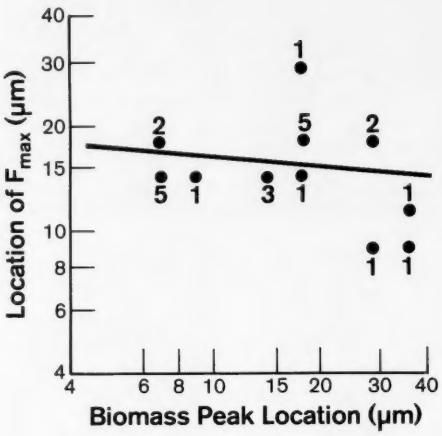


FIG. 3. Correlation between size category of F_{max} and size category of maximum seston concentration. Slope is −0.100 and is not significantly different from zero (r = 0.231, df = 21). Numbers near points are numbers of repeat observations.

cells with subsequent loss of fragments (Conover 1966; Parsons and Seki 1970; Poulet 1973, 1974; Frost 1977), (3) rejection of particles after chewing and tasting (Poulet and Marsot 1978), and (4) fecal pellet production and breakup (Conover 1966; Poulet 1973, 1974; Nival and Nival 1976; Frost 1977; Paffenhöfer and Knowles 1979). As implied by the mechanisms themselves, the amount of particle production depends on the nature of the particles on which the zooplankton are feeding. With respect to fecal pellet production, digestability of the particles is the important factor. Poorly digestable particles will result in larger and/or more numerous fecal pellets and more fragments from their breakup.

The potential bias on filtering rate vs. particle-size curves and W' vs. particle-size curves from particle production depends not only on the nature of the particles being fed upon, but also on the shape of the particle-size spectrum itself. The importance of spectrum shape will be made clear in the simple model that follows. Assume that an experimenter is using a particle counter to measure changes in concentration of seston in a container in which zooplankton feeding is the only force causing changes in particle concentration. Time rate of change of concentration of particulate material in size category i is

$$(1)\quad \frac{dX_i}{dt} = -(N/V)F_iX_i + (N/V)\sum_j F_jX_jf_{ij},$$

where X_i = concentration of particulate material in size cate-

TABLE 1. Mean values and population standard deviations for water temperature and particle concentration in control containers ($\Sigma\bar{C}_i$), net feeding rate (NFR), gross feeding rate (GFR), NFR/GFR ratio, and F_{max} during different seasons.

Season	N	Water temp. (°C)	$\Sigma\bar{C}_i$ (10^6 μm^3·mL^{-1})	NFR (10^6 μm^3 · animal^{-1} · d^{-1})	GFR (10^6 μm^3 · animal^{-1} · d^{-1})	NFR/GFR	F_{max} (mL · animal^{-1} · d^{-1})
Spring (Apr. 24–June 11)	5	4.1±2.3	1.04±0.14	1.51±0.65	1.81±0.47	0.80±0.23	4.77±0.41
Spring except for experiment of June 10–11, 1977	4	3.9±2.6	1.06±0.15	1.78±0.29	1.97±0.33	0.90±0.03	4.87±0.41
Midsummer (July 21–Aug. 16)	6	9.1±0.5	1.55±0.34	3.95±1.67	4.29±1.81	0.92±0.04	6.92±2.12
Late summer–fall (Aug. 29–Nov. 8)	12	10.0±1.7	0.74±0.27	1.05±0.36	1.16±0.36	0.89±0.11	4.88±1.87
Late summer–fall except for experiments of Sept. 13–14, 1977, and Oct 25, 1977[a]	10	9.9±1.8	0.82±0.21	1.12±0.34	1.23±0.34	0.91±0.11	4.36±1.50

[a]Seston concentrations on listed dates were diluted to 1/4 × and 1/3 × initial concentrations, respectively.

gory i ($10^6 \mu m^3 \cdot mL^{-1}$), N = number of zooplankton in the container, V = volume of the container (mL), F_i = filtering rate on size category i ($mL \cdot d^{-1}$), $\sum_j$ = summation over all j ($j = 1, 2, \ldots, n$) size categories, and f_{ij} = proportion of particulate material in size category j that will be transformed by zooplankton feeding into particles in size category i. By rearrangement of equation 1, the apparent (instantaneous) filtering rate, F_i^*, is by definition (Gauld 1951)

$$(2) \quad -(V/N)\frac{dX_i}{dt}/X_i = F_i^* = F_i - \sum_j F_j(X_j/X_i)f_{ij},$$

and the bias in having to use F_i^* for an estimate of F_i is

$$(3) \quad F_i^* - F_i = -\sum_j F_j(X_j/X_i)f_{ij}.$$

The X_j/X_i term in equation 3 implies that the shape of the particle-size spectrum can strongly influence the degree of bias caused by particle production. Furthermore, as zooplankton ingest and produce particles, there will be introduced into F_i^* (and W_i') a time variance caused by the changing ratios of X_j/X_i. Intuitively, the magnitude of bias will be greatest in deep valleys and other low points adjacent to large peaks in the particle-size spectrum because of the tendency of zooplankton to transform particles they have removed from a given size category into smaller and larger particles. That is, the first three mechanisms of particle production will always transform particles of a given size into smaller particles, and the fourth will usually yield larger particles. Because degree of digestion may be dependent on food concentration (Lehman 1976), particle production could be worse for higher concentrations of particles.

Particle production is evident when, for a given size category, higher concentrations of particles are found in experimental than in control containers. However, significant biases from particle production cannot be ruled out because particle production is not evident. Evident particle production was quantified by the NFR/GFR quotient, which has a value of less than 1 when evident particle production is occurring. The quotient NFR/GFR averaged about 0.9 for all seasons, a result suggesting that, apparently, particle production generally was not an important feature of these experiments. An exception is the experiment of June 10–11, 1977 (Fig. 1b), that yielded an NFR/GFR ration of 0.39. For this reason, this experiment was not used in the calculation of the overall mean W' curve. Particle addition is seen below 5 μm, a region where the overall mean W' is zero or low. Perhaps particle addition occurred also in the 10- to 20-μm region of the spectrum in this experiment, causing the pecular M-shaped W' curve. Perhaps particle addition also explains the aberrant W' curve of November 9–10, 1977 (Fig. 1l).

This last experiment is best examined in the context of the four experiment series (Fig. 1: j, k, l, m), of which it is part. In all the experiments of this series, there are two major peaks in the control spectrum at ~7 and 18 μm. Notice first that the relative heights of the two peaks vary among experiments. The height of the 18-μm peak decreases relative to the 7-μm peak in going from fresh to 1-d-old water. This change may be explained by growth of the smaller peak and perhaps settling out and subsequent sticking of the larger particles to the bottom of the jug. It is in the experiment with the strongly developed 18-μm peak (November 9–10) that the aberrant W' is found. Comparing the curves in this series, it is seen that the aberrant shape of the W' curve for November 9–10 is caused primarily by a drop in filtering rates in the size categories less than 18 μm rather than by a significant increase in filtering rate on the 18-μm peak. These lowered filtering rates are consistent with the hypothesis that particles from the 18-μm peak were transformed by zooplankton into particles that fell between the peaks. More will be said about this below, where the nature of the seston in this and other experiments is described.

The Nature of the Offshore Seston

A description of the seston available to the zooplankton in the feeding experiments is helpful for understanding the W' vs. equivalent spherical diameter curves because the nature of the seston can affect these curves. First, selection may be dependent on the taste of the seston (Poulet and Marsot 1978; Poulet 1978; Donaghay and Small 1979; Donaghay 1980). Second, as already discussed, particle production, which may bias the pattern of selection, is dependent on the nature of the seston. Third, particle shape could affect the efficiency with which a zooplankter captures and handles a particle of given equivalent spherical diameter.

In discussing the potential influence of particle shape, it is necessary to distinguish between particles captured by filtering and those raptorially seized. Particles for which all dimensions are much smaller than the dimensions of the filtering chamber of a copepod are captured by filtering (Conover 1966; Alcaraz et al. 1980), and they could be filtered at different efficiencies, depending on their shape and their orientation in the water currents within the filter as these currents pass through the filter pores. Particles with one or more dimensions that are large relative to the filter chamber or mouth opening must be seized raptorially and oriented properly for feeding (Conover 1966; Alcaraz et al. 1980). For example, an elongated cell like *Rhizosolenia indica* must be raptorially seized and oriented with its long axis toward the mouth before it can be ingested (Alcaraz et al. 1980).

A qualitative description of the seston found in the control containers at the end of the feeding experiments is shown in Table 2. The object of this description was to characterize dominant small (<15 μm equivalent spherical diameter) and large (>15 μm) seston in terms of their shapes, food quality, and taste. Dominance was determined from approximate estimates of relative abundance (by volume) from scans of the slides at 200 × magnification. The small seston (<15 μm) was dominated by round, ovoid, or pill-shaped particles in 21 out of 23 experiments. Shape was more variable for large seston: 14 out of 23 experiments were dominated by round, ovoid, or pill-shaped particles. The more variable shape of the large seston was caused primarily by colonial diatoms (*Melosira*, *Fragilaria*, *Asterionella*, *Tabellaria*) and elongated unicellular diatoms (e.g. *Synedra*, *Rhizosolenia*). All of these species can be of modest equivalent spherical diameter, and yet be long in one (*Melosira*, *Synedra*, *Rhizosolenia*) or two (*Asterionella*, *Fragilaria*) dimensions. For example, an eight-cell (stellate) colony of *Asterionella formosa*, which has an equivalent spherical diameter of about 15 μm, has a colony diameter of about 100 μm.

TABLE 2. Dominant constituents of seston in control containers of feeding experiments. When numbers appear before constituents, 1 indicates primary dominants, 2 indicates secondary dominants. An asterisk before a date indicates that small seston was dominated by round, pill-shaped, or ovoid particles; an asterisk after a date indicates that large seston was dominated by these shapes. An asterisk after an alga indicates it was the cause of a large peak in the particle-size spectrum.

Date	Nature of seston	
	Small	Large
* May 24–25, 1977	Detritus, flagellates	*Melosira*, pill-shaped centrics,[a] flagellates
June 10–11, 1977	Flagellates, detritus, short *Melosira* chains	1—*Melosira*, *Stephanodiscus* 2—Elongated unicellular diatoms[b]
*July 21–23, 1977	Flagellates, pill-shaped centrics, detritus	1—*Fragilaria* chains, *Tabellaria* chains, *Asterionella* 2—Pill-shaped centrics
Aug. 7–8, 1977	1—Flagellates, detritus 2—*Tabellaria* cells	1—Pill-shaped centrics 2—*Tabellaria* chains, *Asterionella*
Aug. 15–16, 1977	1—Flagellates* (cryptomonads) 2—Detritus, pill-shaped centrics	1—*Cryptomonas** 2—Pill-shaped centrics, *Tabellaria* chains
*Aug. 29–30, 1977	Flagellates, detritus, centrics, *Tribonema* filaments	Flagellates, pill-shaped centrics, *Fragilaria* chains
Sept. 13–14, 1977	1—Detritus, $CaCO_3$ crystals, cryptomonads 2—*Chroococcus*, *Tribonema* filaments	1—*Cryptomonas* 2—*Coelosphaerium*, *Gomphosphaeria*, *Ceratium*, *Asterionella*
Oct. 25–26, 1977		
Oct. 27–28, 1977	1—Cryptomonads and other flagellates 2—Detritus, coccoid greens, *Chroococcus*	1—*Cryptomonas*, pill-shaped centrics 2—*Fragilaria*, *Melosira* *Asterionella*, *Gomphosphaeria*
Nov. 7–8, 1977		
Nov. 8–9, 1977		
Nov. 9–10, 1977		
Nov. 10–11, 1977	1—Flagellates* 2—Detritus, coccoid greens	1—*Cryptomonas* 2—Pill-shaped centrics, *Fragilaria*, *Asterionella*
Nov. 23–24, 1977	1—Detritus, flagellates 2—Coccoid greens	1—Pill-shaped centrics, *Fragilaria*, flagellates 2—*Tabellaria* chains, elongated unicellular diatoms
Apr. 24–25, 1978	Centrics, detritus, flagellates	*Stephanodiscus**
Apr. 27–28, 1978	1—Centrics, detritus, flagellates 2—Elongated unicellular diatoms	1—*Stephanodiscus** 2—*Melosira*
May 31–June 1, 1978	Detritus, centrics, elongated unicellular diatoms	Elogated unicellular diatoms, pill-shaped centrics, *Melosira*, *Fragilaria*
*July 25–26, 1978		
*July 25–26, 1978		
*July 25–26, 1978	1—Pill-shaped centrics, detritus 2—*Asterionella* cells, elongated unicellular diatoms	1—Pill-shaped centrics, *Fragilaria*, *Tabellaria* 2—*Synedra*, *Asterionella*
*Sept. 20–22, 1978	$CaCO_3$ crystals, flagellates, centrics, coccoid greens, detritus	1—Pill-shaped centrics, elongated unicellular diatoms 2—*Tabellaria*, *Anabaena*
Oct. 17–18, 1978	1—Detritus, cryptomonads, $CaCO_3$ crystals 2—*Chroococcus*, pill-shaped centrics	1—Pill-shaped centrics 2—*Tabellaria* chains, *Melosira*, *Anabaena*, *Coelosphaerium*, *Coelastrum*
Nov. 6–8, 1978	1—Detritus 2—Cryptomonads, *Chroococcus*, pill-shaped centrics, $CaCO_3$ crystals	1—Pill-shaped centrics, *Nephrocytium* 2—*Melosira*, *Anabaena*, *Gomphosphaeria*

[a]Pill-shaped centrics mean unicellular centric diatoms having the shape of a pill (e.g. *Stephanodiscus*, *Cyclotella*).
[b]For example, *Synedra*, *Rhizosolenia*, *Diatoma*.

Food quality and, presumably, taste varied with season. Generally, food quality was lowest in late summer and fall, during which period calcite crystals and organic detritus strongly dominated the smaller seston. Also at this time, green and blue-green algae often were secondary dominants of both large and small seston. A notable exception, however, was the series of experiments of November 7–11, 1977, whose seston was dominated by flagellates and diatoms. During spring and midsummer, flagellates and diatoms were important dominants of small and large seston, respectively. The low average F_{max} observed for late summer and fall (in contrast to the higher F_{max} obtained for midsummer at the same temperature and higher food concentrations) may be an immediate response to poor food quality (Mullin 1963; Gliwicz 1969) or a long-term physiological adaptation to the lower quality of food and its particular biochemical composition (Mayzaud and Poulet 1978).

The seston found in the spring and midsummer experiments strongly suggests that particle shape and fragmentation explain much of the deviation of the few W' curves that varied appreciably from the mean overall W' curve. Especially noteworthy is the dominance by *Melosira* spp. in the experiment of June 10–11, 1977, which yielded the peculiar M-shaped W' curve and the low NFR/GFR value of 0.39. Raptorial selection and/or fragmentation of the *Melosira* chains was probably responsible for this odd pattern of selection. The elongated algae that dominated the experiment of May 31–June 1, 1978, were probably responsible for the rapid decrease in W' beyond 20 μm. In this case, the larger algae may have been too long for efficient handling. Because of the diversity of algae that dominated the large seston in the experiment of November 9–10, 1977, any or all of the mechanisms of particle production may have operated there.

With respect to shape, the experiments of April 24–25 and 27–28, 1978, are of particular interest in that pill-shaped diatoms of the genus *Stephanodiscus* dominated both large and small seston. These experiments, therefore, are quite similar to those of Frost (1972, 1977) done with mixtures of pill-shaped diatom clones. The species of *Stephanodiscus* present had the shape of discs with a thickness to diameter ratio of about 0.36. The peak in the 32- to 40.3-μm size category corresponded to *Stephanodiscus* having a modal valve-view diameter of 50 μm. It is probable that *Stephanodiscus* of this diameter cannot be swallowed whole since *Diaptomus oregonensis*, which is slightly smaller than *D. sicilis*, has a labial palp cleft (through which food enters the mouth) width of 25 μm (Friedman 1977). Most of the fecal pellets found in the experimental containers at the end of these experiments had whole tests of large *Stephanodiscus*. *Stephanodiscus* tests having valve-view diameters up to 30 μm were common, with the largest test having a diameter of 35 μm. In addition, no identifiable fragments of large tests were seen in the fecal pellets. These results suggest that *D. sicilis* was not able to use efficiently the peak of large *Stephanodiscus* because of problems in handling, chewing, and swallowing *Stephanodiscus* of this diameter. Handling large *Stephanodiscus* might be complicated by their marginal spines, which might injure mouth parts of *Diaptomus* during handling necessary for breaking open the tests.

An interesting contrast to the April 1978 experiments is the July 25–26, 1978 (Fig. 1, r–t), set of experiments, which shows appreciable feeding beyond 35 μm. *Fragilaria* and *Tabellaria* dominated the larger-than-35-μm seston, and large fragments of single cells of these species were very common in the fecal pellets. It seems likely that *D. sicilis* was able to handle these colonial forms more efficiently than *Stephanodiscus* because it could break up the colonies into smaller pieces and ingest them as large fragments of whole cells.

The conclusion that emerges from the feeding experiments of late summer and fall is that food quality does not seem to have a strong influence on the general pattern of selection. The worst food quality was found in experiments of September 13–14, 1977; November 23–24, 1977; September 20–22, 1978; October 17–18, 1978; and November 6–8, 1978. In all these experiments, detritus or $CaCO_3$ crystals strongly dominated the small seston, and blue-green algae were occasional secondary dominants of small and/or large seston. Despite the food quality, these W' curves were not very different from the mean overall W' curve. Interestingly, all of the fecal pellets found in the experimental containers of the September 20–22, 1978, experiment were packed with $CaCO_3$ crystals. Details of these observations on ingestion of $CaCO_3$ crystals will be given elsewhere.

Discussion

Diaptomus sicilis feeding on offshore Lake Michigan seston during three different seasons over a 2-yr period exhibited a relatively invariant pattern of particle-size selection that is inconsistent with peak tracking. These results are remarkable in that this invariant pattern persisted for different feeding rates under varying conditions of particle-size spectrum shape and particle abundance. Furthermore, passive, mechanical selection was supported by ingestion of $CaCO_3$ crystals and the similarity of W' curves in periods of low food quality to the overall mean W' curve. The shape of the W' curves is in itself suggestive of passive, mechanical selection: the left-hand limb may result from increasing intersetule and intersetal retention with size (Boyd 1976; Nival and Nival 1976, 1979; Frost 1977), and the right-hand limb from difficulties handling and ingesting large particles. The pattern of selection and consistency of the pattern resemble results obtained by Vanderploeg and Scavia (1979a) for *D. oregonensis* from analysis of their own data from three feeding experiments with natural seston and McQueen's (1970) data from feeding experiments with natural seston and with mixtures of diatoms.

Most of the few experiments that yielded W' curves that differed appreciably from the overall mean W' curve were dominated by elongated (in one or two dimensions) particles that could have been seized raptorially (Alcaraz et al. 1980). Usually the elongated algae were colonial diatoms. Very abundant, evident particle production in the experiment of June 10–11, 1977, in which *Melosira* was the dominant alga, suggests that particle production from fragmentation of colonial diatoms was probably an important bias in experiments with colonial diatoms. Thus, some of the deviation associated with elongated algae may have been caused by fragmentation of colonial forms.

For the purpose of gaining further insights into the

mechanisms of feeding by *D. sicilis* and, perhaps, making generalizations about zooplankton feeding, it is useful to compare my results with those of other studies and attempt a synthesis of copepod feeding. This synthesis will be restricted mostly to the *Calanus*-like copepods because they all pump water through a fixed maxillary filter, and there is no evidence from laboratory studies that suggests greatly differing behavioral or sensory adaptations among these taxa. Moreover, it will be useful to distinguish between laboratory studies of feeding and studies with natural seston.

Laboratory studies of feeding of *Calanus pacificus* in mixtures of pure cultures of similarly tasting, pill-shaped (nearly round) diatoms of different sizes over a 15- to 24-h time period yielded a relatively constant pattern of W' vs. particle size on these mixtures (Frost 1977). Runge (1980) obtained a very invariant W' vs. particle-size pattern for previously starved *C. pacificus* in short-term (<7 h) feeding experiments in mixtures of pill-shaped diatoms; however, Runge obtained lower filtering efficiencies for small diatoms than those predicted from Frost's (1972) filtering rate data obtained in long-term (2−5 d) feeding experiments with single clones of diatoms. Because respective filtering efficiencies for large and medium-sized particles in both studies were the same, Runge concluded that *Calanus* becomes more efficient at handling small diatoms after acclimation. Acclimation or preconditioning effects of the same kind appear to have occurred in a pair of experiments that Harvey (1937) reported for *Calanus* feeding on two species of diatoms of different sizes. In contrast, Marshall and Orr (1955) and Mullin (1963) found no evidence of preconditioning for *Calanus* feeding in mixtures of different algae. Thus, it seems reasonable to conclude that the same species-specific apparently passive, mechanical pattern of selection will be exhibited in preconditioned *Calanus*-like species in mixtures of good-tasting, round (or nearly round) species of algae. However, the significance of preconditioning is unclear for short-term experiments.

Filtering currents set up by *Calanus*-like copepods bring particles of both high and low food quality into the filter chamber (Easterly 1916; Cannon 1928; Lowndes 1935; Friedman 1977). Contact chemoreceptors found in the setae of the first maxillary endites and mandibular endites probably monitor particle taste for rejection (Friedman and Strickler 1975; Friedman 1977). One method that suggests how particles accumulated by the filter are rejected is suggested by Friedman (1977) in his study on *Diaptomus pallidus* in suspensions of 10- to 20-μm plastic microspheres. Microspheres captured by the filter were swept anteriorly in the filtering chamber and accumulated against the endite setae of first maxillae, which form a gate between the filter chamber and mouth. These accumulated microspheres were rejected by a backward flip of the endites. Food quality also may have been monitored for later rejection by the setae of the second maxillae as the particles made contact with the setae, since these setae contain numerous chemosensory pores (Friedman and Strickler 1975). That the contact chemoreceptors of mandibular endites can be used to reject particles while chewing is suggested by Conover's (1966) observations that *Calanus hyperboreus* rejects a raptorially seized fecal pellet after biting off its end. In this regard, Poulet and Marsot (1978) present evidence that *Acartia* and *Eurytemora* can reject particles after chewing them.

Despite these observations, *Calanus*-like copepods appear to have limited abilities to reject particles they have filtered on the basis of taste when these particles are mixed with good-tasting algae. The ingestion of large quantities of $CaCO_3$ crystals by *D. sicilis* has already been noted. Although *C. pacificus* will reject large plastic microspheres (>50 μm), they passively and mechanically ingested microspheres of small and medium sizes with the same respective efficiencies they did algae of small and medium sizes in mixtures of microspheres and algae in feeding experiments of 1.5 h duration (Frost 1977). Limited powers of selection by taste for the diaptomid copepod *Eudiaptomus graciloides* were suggested by its ingestion of great quantities of sand and diatomite during 3- to 10-h expsure to mixtures of sand, diatomite, and lake seston (Gliwicz 1969). Paffenhöfer (1972) observed in long-term feeding experiments (>10 d) with mixtures of red mud and algae that *Calanus helgolandicus* ingested great quantities of red mud and produced numerous fecal pellets containing mainly red mud. In view of the observations of Donaghay and Small (1979) and Donaghay (1980) that *Acartia* becomes more efficient at rejecting inert particles in mixtures of inert particles and algae as time of exposure increases, it would be interesting to know whether the passive, mechanical selection of inert particles observed by Frost (1977) would be strictly adhered to after long exposure to the mixtures of microspheres and algae. Donaghay (1980) notes, however, that experiments performed in his laboratory suggest that *Calanus*, in contrast to *Acartia*, appears to be much more limited in the extent to which behavior may be used to modify filtering patterns.

In my experiments, *D. sicilis* probably was acclimated to the seston on which it fed in most cases. First, during the sorting period, the zooplankton were sorted into prefeeding water identical with that used in the feeding experiments, which were of long (19−29 h) duration. Second, experiments were generally set up on the same day the zooplankton were captured, with water having a particle-size spectrum similar to that found at their depth of capture. Although *D. sicilis* was collected from a broad depth range, particle-size spectra did not usually vary much with depth, especially in the hypolimnion.

The evidence above suggests that an acclimated *Calanus*-like copepod will yield an invariant pattern of selection in mixtures of round or nearly round particles when the large particles are of high food quality and when at least some of the small particles are of high food quality. In view of the predominance of round particles and the high food quality of large particles in Lake Michigan, it is not surprising that *D. sicilis* yielded a fairly invariant pattern of selection. A corollary to this logic is that the W' curves for *D. sicilis* in experiments with mixtures of various proportions of pure cultures of good-tasting (and digestable) round algae of different sizes should be very similar to the overall mean W' curve for lake seston. Experiments with mixtures of *Chlamydomonas* spp. yielded W' curves that were quite similar to the mean overall W' curve for lake seston (Fig. 2). Details of these experiments will be reported elsewhere.

The conclusion of some investigators (Poulet 1973, 1974,

1978; Poulet and Chanut 1975; Cowles 1979) that *Calanus*-like copepods preferentially select peaks in natural particle-size spectra may, in part, result from use of inappropriate measures (or definitions) of selection by these and other investigators. Frost (1977), in discussing Poulet's (1973, 1974) electivity (E) curves for *Pseudocalanus minutus*, has argued that many of them support the concept of passive, mechanical selection. Possibly some of the variability in the E curves results from the dependence of E on both the shape of the particle-size spectrum and the amount of food eaten (Boyd 1976; Vanderploeg and Scavia 1979a, b). This dependence will manifest itself even when grazing is strictly passive and mechanical or is invariant when defined in terms of W'. Moreover, the mathematical technique later used by Poulet and Chanut (1975) to demonstrate peak tracking in Poulet's (1973, 1974) data was not adequate for this purpose (Frost 1977). This same criticism applies to the very similar mathematical technique used by Cowles (1979). When Cowles' (1979) data are presented as efficiency of filtration $[(\bar{C}_i - Z_i)/\bar{C}_i]$, which is roughly proportional to W' (Vanderploeg and Scavia 1979a), it can be seen that filtration efficiency generally increases with size and then generally ultimately decreases (Boyd unpublished data), a pattern not inconsistent with that observed for *D. sicilis*.

Despite incorrect interpretation of many results because of methods of presentation, the overall picture that emerges from these other studies of *Calanus*-like species feeding on natural seston is that often passive, mechanical selection seems to be operating, but that there are specific, sometimes striking, examples of apparent selection of peaks in the particle-size spectrum. Such a striking example can be seen in fig. 3 and 4 of Poulet (1978). During June, there was a single, roughly bell-shaped particle-size spectrum centering around 15 μm. During September, there were enormous twin peaks at 3 and 50 μm that rose an order of magnitude above the concentration of particles in other size categories. For *P. minutus* and most of the copepod species Poulet used, he obtained efficiency of filtration curves with the June water that look very much like the W' curves that were obtained for *D. oregonensis* (Vanderploeg and Scavia 1979a) and *D. sicilis*. For the September spectrum, efficiencies were higher for the peaks than for the region between peaks. He argues that this latter pattern is behavioral selection of biomass peaks.

An alternate explanation of the peak tracking implied by the September efficiency curves is particle production by the zooplankton. Considering the enormity of the peaks in the September spectrum, only a small percentage of the peaks would have to have been converted to particles of other sizes to have masked grazing between the peaks. Unfortunately, Poulet (1978) did not give particle-size spectra for both control and experimental containers. Thus, it is impossible to see if there was evident particle production. The seston in these particular experiments was not described, so it is impossible to make inferences about the seston's potential for particle production.

Because the pattern of particle selection was more invariant in my study than in these other studies with natural seston, it necessarily follows, if this alternate explanation is correct, that particle production was a more significant phenomenon in these other studies than in mine. Particle production is evident to varying degrees in many of the studies that use the Coulter counter to measure grazing (Parsons et al. 1967; Parsons and Seki 1970; Poulet 1973, 1974, 1978; O'Connors et al. 1976; Nival and Nival 1976; Frost 1977; Richman et al. 1977, 1980; Cowles 1979). The recent experiments of Richman et al. (1980) with three different species of *Diaptomus* show, both in feeding experiments with natural seston from Green Bay, WI, and in experiments using mixtures of cultures of species of green algae, many examples of gross particle production, as evidenced by much higher concentrations of particles in the control bottles than in experimental bottles for certain regions of the particle-size spectrum. Low food quality would be expected for Green Bay, where in addition to organic and inorganic detritus, an abundance of green and blue-green algae would be expected (Tarapchak and Stoermer 1976), which could be poorly digested (Porter 1977). This poorly digested material could have contributed to particle production through fecal pellet production. In addition, some of this low quality food could be rejected after chewing because of undesirable taste (Poulet and Marot 1978), producing smaller particles that would mask grazing on smaller size categories. Because of this gross evident particle production, I have not attempted to make inferences about selective feeding of *Diaptomus* from the study of Richman et al. (1980).

Specific examples of evident particle addition also can be seen in the figures of Poulet (1974) and Cowles (1979). Evident particle production showed up in valleys between large peaks or in low points at the bases of large peaks. All these observations are consistent with the hypothesis that particle production caused the apparently varying patterns of food-size selection. It is important to remember that particle production can exert a marked influence on results without showing up as higher concentrations in experimental containers (Eq. 3). Poulet (1974, 1978) and Cowles (1979) may have had more trouble with particle production than I because many of their spectra, like Poulet's (1978) September spectrum discussed above, were characterized by enormous peaks and deep valleys. Much of the particulate material in Poulet's studies (1973, 1974, 1978) was nonliving (Poulet 1976), and a wide variety of algae of different shapes and taxa were present, including delicate chain-forming algae on a few occasions (Poulet 1974: fig. 6). Thus, all four mechanisms of particle production could have been operating in these studies. The seston in Cowles' (1979) study was not described.

Another possible explanation for peak tracking in some experiments with natural seston is the shape of particles in these studies. Elongated particles of both small and large volumes were common in the studies of Poulet (1973, 1974, 1978) as evidenced by photomicrographs of seston in Poulet's (1974) study. As with particle production, the importance of shape cannot be evaluated since the seston was usually not described. As indicated above, the filtering efficiencies of round and elongated particles of small volume could be different, and raptorial capture is required for elongated particles of modest to large volume.

From the discussion above, it would appear there is little if any clear-cut evidence for peak tracking being a major mode of feeding in *Calanus*-like copepods. This is not to say these copepods are robots incapable of making choices on the basis of taste. Nor would I argue that there are no subtle patterns of behavioral selection behind some of the W' curves of *D.*

sicilis. I do, however, argue that there are limits on the sensory and behavioral capabilities of *Calanus*-like copepods that resulted in the relatively invariant pattern of particle selection observed for *D. sicilis*. A large component of feeding of *Diaptomus* and other *Calanus*-like copepods is probably explained by the largely passive and mechanical filter-feeding mode, in which the copepods have limited capacity to distinguish by taste between particles they have collected on their filters when good and poor tasting particles occur in mixtures together. Rejection of large microspheres in Frost's (1977) study and fecal pellets in Conover's (1966) study, and observations of Poulet and Marsot (1978) suggest taste becomes a consideration for larger particles, whatever their mode of capture happens to be. The significance of the raptorial mode of feeding to the overall process of selective feeding is not understood. *Calanus hyperboreus* sometimes raptorially seized the large diatom *Coscinodiscus* if it made contact with its mouthparts (Conover 1966). Alcaraz et al. (1980) showed that *Rhizosolenia* could be raptorially seized if it came within a certain distance of the mouthparts of *Eucalanus*, and that the algae were perceived chemically. Considering the chemosensors possessed by the mouth parts, a chemical sense was probably used for raptorial capture by *C. hyperboreus* as well. Conover (1966) showed that *C. hyperboreus* that had been filtering small cells was reluctant to seize *Coscinodiscus*, thus suggesting threshold and/or preconditioning effects that involve the copepod's chemosensors.

Conceivably, a *Calanus*-like copepod would be able to scan a large volume of water for capture of large algae depending on its swimming speed and the probability of sensing and capturing particles as a function of distance from the mouth parts for a given swimming speed (Conover 1966; Alcaraz et al. 1980). This probability would be higher for larger particles since they would give off a stronger scent. In this regard, it is theoretically possible for a copepod to exhibit an invariant pattern of particle-size selection using both filtering and raptorial modes of feeding in mixtures of good-tasting, round algae. In this case, the rate at which water is pumped through the filter must remain constant relative to the rate at which particles are encountered in the raptorial feeding mode. This hypothetically constant pattern also may apply to the case in which some of the small and medium-sized particles are of poor food quality. Thus, the constant patterns of selection in my study and the studies of Frost (1977) and Runge (1980) do not necessarily rule out a significant raptorial component of feeding.

In conclusion, the conservative patterns of size selection revealed by *D. sicilis* in offshore Lake Michigan and by other *Calanus*-like species in laboratory experiments are consistent with the simple mechanisms reviewed here, thus implying we are close to understanding and quantifying food selection by these copepods. In addition, the potential biases of particle shape and production discussed herein suggest that future research should be conducted under conditions in which particle shape is known and the influence of particle production minimized. Lastly, the study of feeding in offshore Lake Michigan revealed potential effects of seasonal food quality on ingestion rate of *D. sicilis* that warrant further study. Because of the strong interaction between particle selection and ingestion rates (Vanderploeg and Scavia 1979a), these processes must be studied together.

Acknowledgments

I thank S. J. Tarapchak and E. F. Stoermer for help in identification of the seston. I thank D. Scavia, C. E. Boyd, P. L. Donaghay, G. R. Harbison, G. -A. Paffenhöfer, S. J. Tarapchak, J. Bowers, L. Herche, and A. Robertson for their helpful comments on the manuscript.

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Reduction, Methylation, and Incorporation of Arsenic into Lipids by the Marine Phytoplankton *Dunaliella tertiolecta*

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WRENCH, J. J., AND R. F. ADDISON. 1981. Reduction, methylation, and incorporation of arsenic into lipids by the marine phytoplankton *Dunaliella tertiolecta*. Can. J. Fish. Aquat. Sci. 38: 518–523.

The metabolism of arsenate by the unicellular marine phytoplankton *Dunaliella tertiolecta* was studied using the isotope ^{74}As. During a 45-min-exposure period the algal cells synthesized three polar arsenic metabolites which were identified as arsenite, monomethylarsonic acid, and dimethylarsinic acid. A large fraction of assimilated arsenic appeared in the lipid fraction and three arsenolipids could be separated by thin-layer chromatography. The turnover of dimethylarsinic acid and arsenolipids was rapid since all four metabolites reached equilibrium levels within the exposure period. Two of the arsenolipids were found to be labile in acid solution, and the primary acid hydrolysis product in both cases was identified as arsenite. One of these acid-labile arsenolipids behaved as an anionic compound on diethylaminoethyl cellulose ion-exchange columns and was also susceptible to hydrolysis by phospholipase D. A chromatographically identical compound could be synthesized from phosphadityl inositol and arsenite. The acid-labile anionic phosphatide produced by algae is therefore proposed to be a complex between arsenite and phosphadityl inositol.

Key words: arsenic, arsenite, dimethylarsinic acid, phytoplankton, arsenolipids, phosphadityl inositol

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Les auteurs se sont servi de l'isotope ^{74}As pour étudier le métabolisme des arsenates par le phytoplanctonte marin unicellulaire *Dunaliella tertiolecta*. Lors d'une période d'exposition de 45 min, les cellules algales synthétisèrent trois métabolites d'arsénic polaires identifiés comme étant arsénite, acide monométhylarsénique et acide diméthylarsénique. Une importante fraction de l'arsénic assimilé apparut dans la fraction lipidique, et la chromatographie en couche mince a permis de séparer trois arsénolipides. Le renouvellement de l'acide diméthylarsénique et des arsénolipides fut rapide puisque les autres métabolites atteignirent tous des niveaux d'équilibre pendant la période d'exposition. On a constaté que deux des arsénolipides étaient labiles en solution acide et, dans les deux cas, le produit de l'hydrolyse acide primaire a été identifié comme arsénite. Un de ces arsénolipides labiles à l'acide se comporte comme un composé anionique sur des colonnes échangeuses d'ions de cellulose diéthylaminoéthyl et est également susceptible à l'hydrolyse par la phospholipase D. On a pu synthétiser, à partir de phosphadityl inositol et d'arsénite, un composé chromatographiquement identique. Nous suggérons donc que le phosphatide anionique labile à l'acide produit par les algues est un complexe entre l'arsénite et le phosphadityl inositol.

Received August 8, 1980
Accepted January 14, 1981

Reçu le 8 août 1980
Accepté le 14 janvier 1981

BIOCHEMICAL modification of inorganic arsenic is a fundamental factor determining the environmental chemistry of this element. In marine waters the principal dissolved form is arsenate (As V); however, during phytoplankton blooms significant reduction to arsenite (As III) has been observed (Johnson and Burke 1978). Similarly, a positive correlation has been established between primary production in the photic zone and levels of dissolved methylated arsenic derivatives (Andrae 1979).

Marine biota maintain steep concentration gradients for arsenic (Leatherland et al. 1973) and the levels in some

Printed in Canada (J6185)
Imprimé au Canada (J6185)

organisms are remarkably high, sometimes over 100 $\mu g \cdot g^{-1}$ dry weight (LeBlanc and Jackson 1973; Bohn 1975; Kennedy 1976). Since the toxicity of arsenic is highly dependent upon speciation it is clearly important from the public health point of view to determine the chemical forms of arsenic which are present in marine organisms and to investigate their behavior in food webs. In this respect most attention has focused on organisms at the lower trophic levels. Arsenic in marine algae is known to be concentrated in the lipids (Lunde 1972) in a form which is efficiently transferred along experimental food chains (Wrench et al. 1979). Detailed examinations of the chemical nature of arsenic in the lipid fraction have identified arseno-analogues of phosphatides in which the nitrogen in choline or serine moieties is replaced by arsenic (Irgolic et al. 1977; Bottino et al. 1978a; Cooney et al. 1978). These observations imply a biochemical pathway of at least eight steps whereby arsenic is reduced and then methylated to arsine, which reacts with products of intermediary metabolism to form complexes which are subsequently esterified as choline or serine analogues with diacylglycerols (Cooney et al. 1978).

Much of the work on identification of arsenolipids has, by necessity, dealt with water-soluble arsenic compounds released from lipids by acid hydrolysis or alkaline deacylation. In this work we have investigated the possibility that arsenic in algal lipid extracts may be in a form which would be destroyed by rigorous chemical degradative procedures, or even by exposure to complexing agents. Although we have obtained algal cells by standard culture methods, we have avoided carrying out experiments on algae in culture since the medium, although well defined, contains high levels of potentially interfering ions, notably phosphate, and also chelating agents such as ethylenediaminetetraacetic acid (EDTA). The work described in this paper further differs from previous investigations in that it deals with events occurring during the first 45 min of exposure of cells to arsenic.

Methods

Pure cultures of the marine chlorophyte *Dunaliella tertiolecta* were grown at 10°C in f/2 medium (Guillard and Ryther 1962). Routine plating of mature algal cultures revealed no evidence of bacterial contamination. Phytoplankton were recovered from culture by centrifugation at 8000 g and 10°C for 5 min. Microscopic examination of cells obtained by this method showed that motility was largely unimpaired, indicating that the algae survive the harvesting procedure. Algal cells were resuspended in 25 mL of sterile 0.45-μm-filtered seawater spiked with 0.2 MBq of carrier-free ^{74}As as arsenate (Amersham Searle Ltd.) and incubated at 10°C for 45 min.

Extraction and Chromatography

Cells were recovered from incubation medium by filtration onto a glass fiber filter and were washed with 20 mL of filtered seawater. All solvents subsequently used in extraction and chromatography of arsenic metabolites were of reagent grade and were redistilled from glass. The filter was extracted with 6 mL of chloroform/methanol (2/1, v/v) followed by 1.5 mL of distilled water. After separation of the emulsion by centrifugation, the upper water/methanol and lower chloroform phases were removed, evaporated to 0.1 mL under reduced pressure, and stored at −4°C under nitrogen.

Chloroform extracts containing algal lipids were chromatographed on deactivated 250-μm silica gel GF thin-layer chromatography (TLC) plates using either chloroform/methanol/water (70/30/5, v/v/v) or chloroform methanol/water/ammonia (130/70/8/0.5, v/v/v/v) as the developing solvent. Water/methanol extracts were chromatographed either on 250-μm MN 300 cellulose TLC plates with an eluant of methanol/*n*-butanol/water (3/1/1, v/v/v) or on Whatman No. 4 paper with phenol/water (100/40, wt/wt) as the eluant.

Polar lipids used in chromatography as standards were phosphatidyl choline, phosphatidyl serine, phosphatidyl ethanolamine, lyso-phosphatidyl choline, phosphatidyl inositol, sphingomyelin, plant sulfatides, cerebrosides (Supelco Inc.), mono- and di-galactosyl diglycerides, and bovine ceramides (Applied Science Inc.)

Standards for arsenic were sodium arsenate, sodium *m*-arsenite, monomethylarsonic acid (MMAA), and dimethylarsinic acid (DMAA) (Sigma Chemical Co.).

The distribution of radioactivity in thin-layer chromatograms was monitored on a Panax TLC plate scanner equipped with a windowless G-M tube. When radioactivity in chromatograms was too low to be detected by this method, or when quantitation of radioactivity was required, appropriate areas of TLC plates were removed and counted in 15 mL of a toluene-based aqueous fluor on a liquid scintillation counter with an open window.

Hydrolysis of Lipid Extracts

Individual arsenic metabolites in the lipid extracts were hydrolyzed by suspending appropriate areas of developed chromatograms in 1.5 mL of 0.1 mol/L HCl. The suspension was heated at 90°C for 30 min and extracted with 6 mL of chloroform/methanol (2/1, v/v). Hydrolysis products in the aqueous methanol phase were chromatographed as described above.

Replicate samples of whole lipid extract were subjected to enzymatic hydrolysis with phospholipase D (Sigma Chemical Co., 100 units/mg). Substrate for these experiments consisted of 0.1 mL of lipid extract, 1 mL of ether, 1.5 mL of 0.1 mol/L acetate buffer (pH 5.6), and 0.1 mL of 1 mol/L $CaCl_2$ (Ansell and Hawthorne 1964). The hydrolysis was initiated by addition of 0.5 mg of enzyme, or in the case of blank replicates by addition of 0.5 mg of a nonenzymic protein (human serum albumin). Samples were incubated at 20°C for 6 h and then extracted with 6 mL of chloroform/methanol (2/1, v/v). The chloroform phase was rechromatographed as described above.

Separation of Glycolipids and Phospholipids

Silicic acid columns (20 cm × 1 cm) were prepared as described by Vorbeck and Marinetti (1965). Stepwise elution of the components of algal lipid extracts was carried out with chloroform/acetone (1/1, v/v, 5-column volumes), acetone (10-column volumes), chloroform/methanol (95/5, v/v, 10-column volumes), chloroform/methanol (80/20, v/v, 20-column volumes), and methanol (10-column volumes)

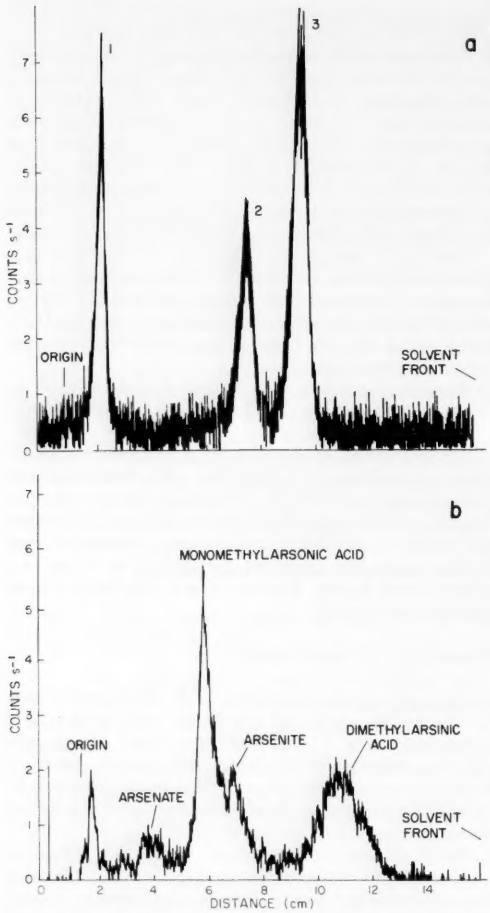

FIG. 1. Arsenic metabolites synthesized by *Dunaliella* during 45-min exposure to ^{74}As as arsenate. (a) Chromatogram of ^{74}As in lipid (chloroform) extract. Sample developed on 250-μm silica gel GF thin-layer plate with chloroform/methanol/water (70/30/5, v/v/v). Lipid arsenic metabolites 1, 2, and 3. (b) Chromatogram of ^{74}As in nonlipid water/methanol extract. Sample developed on 250-μm cellulose MN 300 thin-layer plate with methanol/butanol/water (3/1/1, v/v/v).

(Christie 1973). Each fraction was evaporated to dryness under reduced pressure, taken up in a small volume of chloroform/methanol (2/1, v/v), and subjected to TLC on silica gel to determine the content of ^{74}As.

Separation of Anionic and Zwitterionic Lipids

Anionic and zwitterionic lipids were separated on diethylaminoethyl (DEAE) cellulose anion-exchange columns (20 cm × 1 cm) (Rouser et al. 1976). Samples of algal lipids were first eluted with 10-column volumes of chloroform/methanol (7/3, v/v) to remove zwitterionic lipids, and then with 10-column volumes of chloroform/methanol/ammonium acetate (4/1/20 mL concentrated aqueous ammonia per litre + 0.05 mol/L ammonium acetate) to remove anionic lipids. Columns tested with standard polar lipids (100 μg) showed that the procedure outlined above achieves good separation between zwitterionic phosphatides, such as phosphatidyl ethanolamine or phosphatidyl choline, and anionic lipids, such as phosphatidyl inositol and plant sulfatides.

Treatment of Arsenolipids with Complexing Agents

Individual arsenolipids in 4 mL of chloroform/methanol (2/1, v/v) were exposed to 1 mL of a solution of 5 mmol/L cysteine in 0.5 mol/L acetate buffer (pH 5.6) by shaking for 2 h. The aqueous methanol phase was evaporated to a small volume and chromtographed on either paper or cellulose thin-layers as described above.

Arsenolipids were shaken with 250 μg of dithizone (diphenylthiocarbazone, Fisher Scientific Co.) in 1 mL of chloroform for 1 h. The sample was evaporated to an appropriate volume and chromatographed on silica gel.

Synthesis of Arsenite-Polar Lipid Complexes

Stock $^{74}AsO_4^{3-}$ solution was reduced to $^{74}AsO_2^-$ by heating 0.2-mBq quantities in 1 mL of ascorbic acid solution (50 mg/mL) on a boiling water bath under reflux for 10 min. The reductate was subjected to TLC on cellulose to separate arsenate, arsenite, arsenic trioxide, and ascorbic acid. The zone which contained arsenite was removed and extracted with 4 mL of 0.05 mol/L carbonate buffer (pH 9.6). Samples of this arsenite solution (2 mL) were added to 8 mL of chloroform/methanol (2/1, v/v) containing standard polar lipid. An emulsion was maintained by shaking for 12 h and then separated by centrifugation. The lower chloroform phase was chromatographed on silica gel. All common phospholipids, mono- and di-galactolipids and hydroxy fatty acids (ceramides), were tested in this way for their ability to form complexes with arsenite.

Results

Typical profiles of ^{74}As in lipid and nonlipid fractions of *Dunaliella* are shown in Fig. 1. The three distinct features observed after TLC of lipid extracts are associated with polar lipid components; no ^{74}As was observed in the solvent front containing the "neutral" lipids (Fig. 1a). Lipid metabolite 1 occurred near the origin and did not correspond to any of the standards examined. Lipid metabolite 2 corresponded to a distinct spot identified as sulfatide. Lipid metabolite 3 ran ahead of ethanolamine phosphatides with a sharply defined analytical feature which reacted positively to a glycolipid disclosing agent (anisaldehyde–sulfuric acid). Cellulose TLC of water/methanol extracts (Fig. 1b) showed four easily identifiable features: arsenate, monomethylarsonic acid (MMAA), arsenite, and dimethylarsinic acid (DMAA). The chromatographically immobile feature near the origin could not be identified.

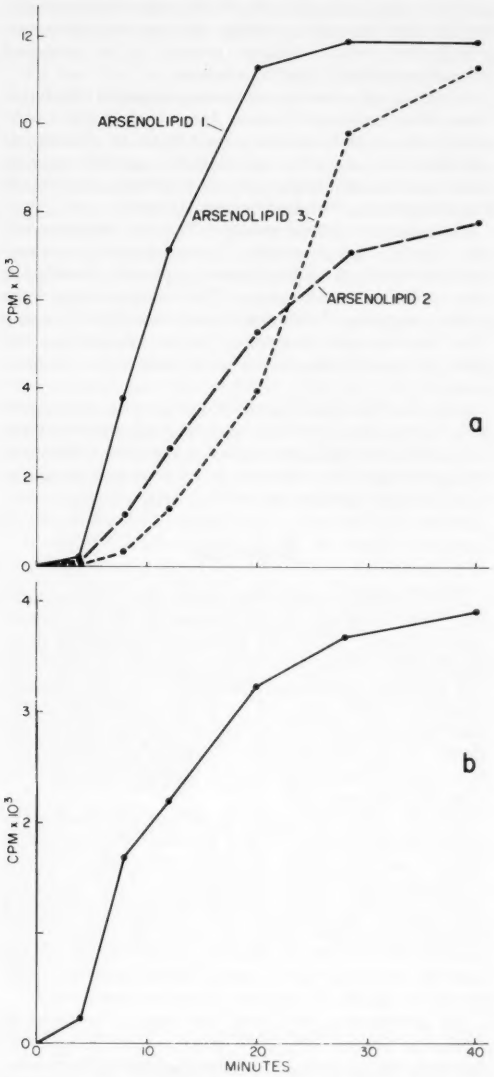

FIG. 2(a). Rate of synthesis of individual arsenolipids by *Dunaliella*. (b) Rate of synthesis of dimethylarsinic acid by *Dunaliella*. CPM = counts per minute.

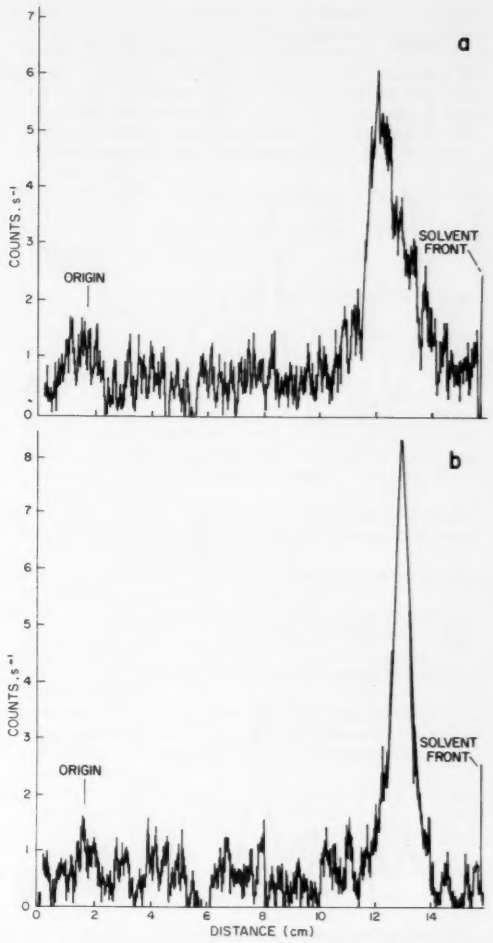

FIG. 3. Chromatographic profiles of ^{74}As released into water/methanol extract after mild acid hydrolysis (0.1 mol/L HCl at 90°C for 30 min) of individual arsenolipids. (a) Single acid hydrolysis product of arsenolipid 1 identified as arsenic trioxide derived from dehydration of arsenite in acid solution; arsenolipid 2 produces an identical compound. (b) Acid hydrolysis product of arsenolipid 3. Samples chromatographed on thin-layer cellulose with methanol/butanol/water (3/1/1, v/v/v) as developing solvent.

The rates of formation of individual arsenolipid metabolites and dimethylarsinic acid (Fig. 2) were characteristically sigmoid.

Arsenolipids 1 and 2 are completely hydrolyzed by 0.1 mol/L HCl. Typical chromatographic profiles (Fig. 3a) of the hydrolysis products of these compounds are identical and show a large peak which does not correspond to any of the forms of arsenic observed in water/methanol extracts. In acid solution arsenite, or arsenious acid, dehydrates to arsenic trioxide; a compact spot corresponding to the position of the large peak in Fig. 3a can be produced by chromatography of a sample of a sodium *m*-arsenite solution (10 mg/mL) in 0.1 mol/L HCl which had been heated to 90°C for 30 min. The acid hydrolysis product of arsenolipids 1 and 2 is therefore identified as arsenite. Arsenolipid 3 was partially hydrolyzed by treatment with 0.1 mol/L HCl to give a single hydrolysis product (Fig. 3b) whose identity has not yet been determined.

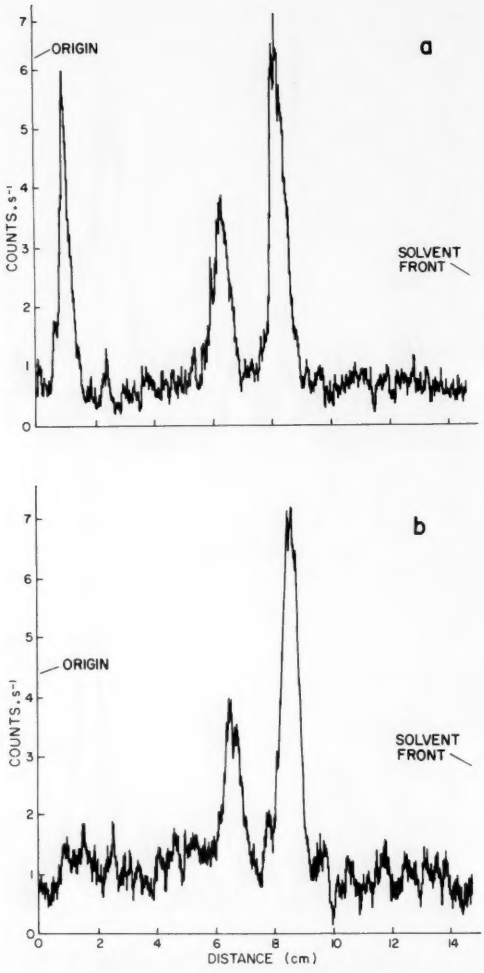

FIG. 4. Effect of phospholipase D on chromatographic profile of arsenolipids showing complete enzymic hydrolysis of arsenolipid 1. (a) Blank incubate containing 0.5 μg of nonenzymic protein (serum albumin). (b) Test incubate containing 0.5 mg of phospholipase D. Samples chromatographed on thin-layer silica gel with chloroform/methanol/water (70/30/5, v/v/v) as developing solvent.

Figure 4 shows the effect of phospholipase D. Under the conditions described above 0.5-mg quantities of the enzyme hydrolyzed 100 μg of all phospholipid standards to produce phosphatidic acid. Arsenolipid 1 was completely hydrolyzed by phospholipase D while arsenolipids 2 and 3 were unaffected.

Attempts to separate glycolipid and phospholipid metabolites of arsenic on silicic acid columns were unsuccessful in the case of arsenolipids 1 and 2. Both compounds were broken down on silicic acid columns. Arsenolipids 3, however, appeared principally in the chloroform/methanol (80/20, v/v) fraction containing ethanolamine and serine phosphatides, with a smaller amount in the preceding chloroform/methanol (95/5, v/v) eluate.

All three lipid metabolites chromatographed on DEAE cellulose anion exchange columns. Arsenolipids 2 and 3 were eluted with neutral and zwitterionic lipids by chloroform/methanol (7/3, v/v) while arseno-lipid 1 was more strongly retained on the column and was eluted with the anionic lipids by chloroform/methanol/ammonium acetate.

Dithizone and cysteine extracted ^{74}As from arsenolipids 1 and 2. In the case of cysteine, ^{74}As is released as a water-soluble form which can be chromatographically identified as arsenite. Dithizone also extracts ^{74}As from arsenolipid 3; on rechromatography of dithizone-treated arsenolipid 3, a new ^{74}As-containing peak is observed near the solvent front; this peak corresponds to the position of dithizone in the chromatogram.

Attempts to synthesize complexes of arsenite and standard polar lipids achieved limited success. The most consistent results were obtained with phosphatidyl inositol; a large peak corresponding to arsenolipid 1 could be observed in samples of phosphatidyl inositol exposed to $^{74}AsO_2^-$.

Discussion

The movement of carrier-free isotope into different metabolic pools essentially reflects turnover in the biochemical system (Kleiber 1955). The turnover of arsenolipid metabolites synthesized by *D. tertiolecta* appears to be rapid since ^{74}As approaches equilibrium levels within 30 min of exposure to labeled arsenate (Fig. 2a). A similar observation can be made with respect to DMAA (Fig. 2b), and since arsenite and MMAA are precusors of DMAA (McBride and Wolfe 1971), these forms of arsenic must also be subject to rapid turnover in the phytoplankton cell.

For most organisms arsenate is the least toxic form of the element (Peoples 1975); in algae, however, where phosphate is often a limiting nutrient, the ability of arsenate to compete in phosphorylation reactions results in a toxic interaction which increases the requirement for phosphorus and reduces the rate of cell division (Bottino et al. 1978b; Sanders 1979). Methylation of arsenic is therefore a detoxication process whereby the introduction of methyl groups produces a compound less capable of inhibiting phosphate esterification.

The incorporation of arsenic into lipids is less easy to rationalize. Cooney et al. (1978) have proposed that the synthesis of arsonium analogues of phosphatides by *Chaetoceros concavicornis* represents a detoxication process. (We have carried experiments on *Chaetoceros* in a similar way to those described for *Dunaliella*. The assimilation of arsenic is very slow compared to that in *Dunaliella* and after an exposure time of 45 min the only metabolites detectable are arsenite and arsenolipid 1). However, the products of methylation, MMAA, and DMAA do not affect diatom productivity and are efficiently excreted into the extracellular medium (Andrae 1978b; Sanders 1979); there is, therefore, no toxicological requirement to metabolize further these compounds to arsonium analogues. It is in fact conceivable that the synthesis of such compounds is an adaptation to limited nitrate availability

in that arsonium phosphatides may function equally well as structural lipids as their choline, serine, or ethanolamine analogues.

We can find no evidence of arsonium compounds in *Dunaliella*. The results of experiments with phospholipase D consistently show that only arsenolipid 1 is a phosphatide. The primary acid hydrolysis product of this compound is arsenite. Cysteine, which acts as a competing ligand for As III, releases arsenite from the intact lipid. These observations suggest that arsenolipid 1 is an arsenite–phosphatide complex. Arsenite, in contrast with pentavalent forms of the element, is capable of forming stable coordinate covalent complexes with a wide range of functional groups normally found in biological systems. The reaction of arsenite with vicinal hydroxyl groups has been applied to the separation of structural isomers of naturally occurring compounds, notably cyclitols, sugars, and hydroxy fatty acids (Frahn and Mills 1959; Karlsson and Pascher 1971). Since we can produce a radioarsenic compound from $^{74}AsO_2^-$ and phosphatidyl inositol which chromatographs in the position of arsenolipid 1, we propose that this compound is a cyclic complex of arsenic and the vicinal 1, 2 hydroxy groups of myo-inositol. Reduced chromatographic mobility of the inositide is probably due to the introduction of a second anionic group into the molecule.

Arsenolipid 2 also appears to be an arsenite complex; however, the resistance of this compound to phospholipase D and its behavior on DEAE cellulose columns suggests a neutral or zwitterionic glycolipid rather than a phospholipid.

Arsenolipid 3 differs from arsenolipids 1 and 2 in that its acid hydrolysis product is not arsenite. This compound is stable on silicic acid columns and is eluted in what is essentially a phosphatide fraction. However, it is possible that the presence of arsenic in the molecule may change the absorption characteristics of a metabolite which appears to be, from its resistance to phospholipase D, glycolipid in nature.

All three arsenolipids synthesized by *Dunaliella* are distinctly different from arsenic metabolites previously reported. In general terms the identification of arsenite–lipid complexes shows that arsenic has rapid access to the lipid pool by a single biochemical process of reduction. The ability of a wide range of organisms, ranging from bacteria to mammals, to carry out this reductive step suggests that arsenite–lipid complexes may be widely distributed throughout the marine ecosystem.

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ADDENDUM: A recent paper (Edmonds and Francesconi 1981) provides strong evidence for the synthesis of arseno-sugars by marine macrophytic algae. This work directly supports our conclusions that arsenic is present in the sugar moiety of algal glycolipids.

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The Prediction of Lacustrine Phytoplankton Diversity[1]

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LAZERTE, B. D., AND S. WATSON. 1981. The prediction of lacustrine phytoplankton diversity. Can. J. Fish. Aquat. Sci. 38: 524–534.

We tested the hypothesis that total phytoplankton biomass can predict phytoplankton community structure independent of its taxonomic composition. From a 2-yr study on Lake Memphremagog, Quebec, which exhibits a marked axial trophic gradient, 133 samples were rarefied to uniform count sizes and a range of diversity numbers, based on proportional biomass, was calculated for each. Biomass is a good predictor of evenness ($0.7 < R < 0.9$), but not species richness ($0.1 < R < 0.3$), and this prediction is independent of changes in taxonomic composition. Species richness is more directly related to season and changes in taxonomic composition.

Key words: diversity, evenness, species richness, phytoplankton

LAZERTE, B. D., AND S. WATSON. 1981. The prediction of lacustrine phytoplankton diversity. Can. J. Fish. Aquat. Sci. 38: 524–534.

L'étude décrite plus bas a été menée en vue de vérifier l'hypothèse que la biomasse phytoplanctonique totale peut servir à prédire la structure de la communauté phytoplanctonique, indépendamment de sa composition taxonomique. L'étude, qui a duré 2 ans, a été effectuée sur le lac Memphrémagog, au Québec, qui exhibe un gradient trophique axial marqué. Un total de 133 échantillons ont été ajustés à des comptages uniformes et, pour chacun, nous avons calculé une gamme d'indices de diversité, fondés sur la biomasse proportionnelle. La biomasse permet de prédire l'uniformité ($0{,}7 < R < 0{,}9$) mais non la richesse en espèces ($0{,}1 < R < 0{,}3$), et cette prédiction est indépendante des changements de composition taxonomique. La richesse en espèces est plus directement liée à la saison et aux changements de composition taxonomique.

Received July 2, 1980
Accepted January 28, 1981

Reçu le 2 juillet 1980
Accepté le 28 janvier 1981

MOST lacustrine phytoplankton communities exhibit substantial temporal changes in community size and structure as measured by standing crop (biomass or chlorophyll *a*), diversity, and taxonomic composition. Attempts to predict quantitatively short- and long-term changes in total phytoplankton standing crop have met with increasing success (Sakamoto 1966; Vollenweider 1968; Dillon and Rigler 1975) using the limiting nutrient load as the predictor. Taxonomic changes, however, are not yet quantitatively predictable, although the abundance of some taxa have been related to season (Lund 1965; Hutchinson 1967) or trophic gradients (Hutchinson 1967; Tarapchak and Stoermer 1976; Nicholls 1976).

It has been hypothesized that the less taxonomically specific aspects of community structure, such as the number of species present (richness) and the relative distribution of biomass (evenness), are predictable independent of the underlying taxonomic composition (Pielou 1975; May 1976; Kempton 1979). This general hypothesis is particularly attractive when applied to the lacustrine phytoplankton; standing crop should be an appropriate choice for an independent variable because of its predictability whereas taxonomic composition should be excluded from any general relationship. It has long been suggested that there exists some inverse association between trophic level (which is related to standing crop of the phytoplankton) and some general measure of phytoplankton diversity, such as the Shannon–Weaver index (Patten 1962; Williams 1964; Margalef 1968; Moss 1973; Eloranta 1976). It remains to be seen just how precise this proposed relationship is, what functional form it takes, and whether it is independent of changes in taxonomic composition.

Specifically, using 2 years of data from a large temperate lake (Lake Memphremagog, Quebec), we tested the hypothesis that total phytoplankton biomass can be used to predict the richness and/or evenness component of phytoplankton community structure, and that this prediction is independent of changes in community composition. We expect that the relationships obtained will be useful in comparing phytoplankton diversity across gradients other than biomass, such

[1]A contribution of the Lake Memphremagog Project, Limnology Research Group.

Printed in Canada (J6138)
Imprimé au Canada (J6138)

as stability or latitude.

Methods

Study Site

Lake Memphremagog is a long (40 km), narrow (mean width, 2.4 km) lake located on the Quebec–Vermont border with a catchment area of glacial origin. A pronounced nutrient gradient traverses the long axis of the lake from South to North (Peters 1979; Fig. 1) which results in parallel changes in primary production (Ross and Kalff 1975) and benthic (Dermott et al. 1977) and fish biomass (Nakashima and Leggett 1975; Gascon and Leggett 1977).

Sampling and Enumeration

Sampling of the phytoplankton community was done on a weekly or bi-weekly basis at four stations situated along the North–South nutrient gradient in Lake Memphremagog (Fig. 1), from May 1976 to October 1977, with only occasional samples taken during the period of ice cover. A total of 133 samples were enumerated. Each collection consisted of an integrated tube sample taken either to the depth of the thermocline, or to a maximum depth of 15 m during unstratified periods. Subsamples were fixed immediately with Lugol's iodine and later enumerated using the Utermöhl inverted microscope technique (Utermöhl 1958). Large taxa of low abundance were counted under low power (225×) across diagonal transects or over half the chamber area; a minimum of 26% of the volume settled was examined. Extremely small or abundant taxa were counted under higher power (450× or 900×) across diagonal transects. Although high power was often necessary to identify taxa to the species level, we were able to count 136 out of 163 total taxa under low power because key distinguishing characteristics were still discernible. For reasons to be discussed later, only these larger taxa (approximately greater than 20 μm diameter) are included in the following analysis. The biomass of each taxon was calculated assuming a density of 1.0 and using volumes estimated from mean dimensions or, for colonial or filamentous taxa, using individual measurements. Counting units were not always randomly distributed within the settling chamber and thus transects were counted across any observed density gradient (Willén 1976). A more detailed description of the methodology and taxonomy can be found in Watson (1979).

Diversity Statistics: Theoretical Derivation

One method of examining changes in diversity is to fit mathematical models to the taxon abundance curves and use the estimated parameters of these models as indices of diversity (Kempton 1979). There is no guarantee, however, that any one model will provide the best fit to all samples under consideration; therefore, changes in the parameters estimated may reflect a lack of fit to the model or real changes in the underlying distribution of abundance, or a combination of these factors. To avoid this uncertainty we employed a range of diversity statistics that are differentially sensitive to the rarest or most common taxa and then evaluated the relationship with total biomass for each. Specifically, we used a modification of Renyi's (1961) family of diversities,

$$H_\alpha = \frac{\log \Sigma P_i^\alpha}{1 - \alpha},$$

where P_i is the proportional importance of each taxon, measured by its relative biomass, and α is an arbitrary con-

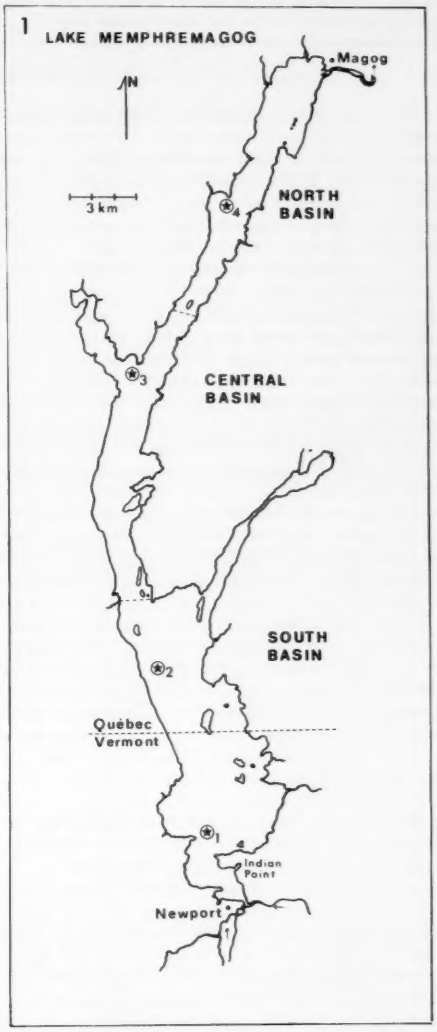

FIG 1. Map of Lake Memphremagog. Sampling stations are indicated by stars. Maximum nutrient levels are found at the south end of the lake.

TABLE 1. The mean ($\bar{x}$), standard deviation (SD), maximum value (Max.), and minimum value (Min.) for the five diversity numbers (N_0–N_2) and biomass for the four different count sizes.

	Diversity nos.											
	N_0				$N_{1/4}$				$N_{1/2}$			
Count size	$\bar{x}$	SD	Max.	Min.	$\bar{x}$	SD	Max.	Min.	$\bar{x}$	SD	Max.	Min.
200	26.4	8.35	47.0	10.3	19.1	5.90	33.9	6.64	14.7	4.60	24.5	4.31
400	32.7	10.1	61.0	13.9	22.5	6.99	38.8	8.34	16.6	5.43	28.0	5.52
800	37.3	10.7	62.0	19.6	24.5	7.69	41.5	10.9	17.6	6.38	30.4	5.98
1600	41.2	11.3	65.7	24.3	25.2	8.13	41.0	12.5	16.9	6.78	29.8	6.86
	N_1				N_2				Biomass			
200	9.96	3.58	16.4	2.51	6.69	2.70	12.5	1.70	1656	1340	6450	255
400	10.7	4.18	18.7	2.84	6.95	3.11	14.3	1.67	1761	1350	6450	271
800	10.9	4.95	21.5	2.76	6.85	3.56	14.4	1.65	2080	1441	6450	359
1600	9.41	5.08	19.4	2.85	5.46	3.38	13.1	1.66	2735	1624	6449	359

TABLE 2. Two examples of the effects of count size on diversity number (N_0–N_2). Day 205 is typical, day 487 is extreme.

	Count size	Diversity nos.						
		N_0	$N_{1/2}$	N_1	N_2	$N_{1/2}/N_0$	N_1/N_0	N_2/N_0
Day 205	200	31.9	18.9	13.2	8.5	0.59	0.41	0.27
	400	39.8	21.7	15.0	9.8	0.55	0.38	0.25
	800	49.1	24.3	16.2	10.2	0.49	0.33	0.21
	1600	56.0	25.2	16.4	10.3	0.45	0.29	0.18
Day 487	200	18.8	13.5	11.4	9.3	0.72	0.61	0.49
	400	25.0	17.2	14.2	11.5	0.69	0.57	0.46
	800	28.8	19.2	15.6	12.2	0.67	0.54	0.42
	1600	31.7	20.7	16.7	13.0	0.65	0.53	0.41

stant. Thus for example,

H_0 = log (n), log of the total number of taxa,
$H_1 = -\Sigma P_i \log (P_i)$, the Shannon–Weaver Index,
$H_2 = -\log (\Sigma P_i^2)$, log of the reciprocal of Simpson's Index,

where H_1 is obtained by taking the limit of H_α as α approaches 1. Using the natural log to define H_α and taking the exponential of H_α gives Hill's (1973) diversity numbers,

$$N_\alpha = (\Sigma P_i^\alpha)^{\frac{1}{1-\alpha}}.$$

Hill's diversity numbers can be regarded as the "effective" number of taxa in the sample for a given α, which we find easier to interpret than the units of Renyi's diversities (e.g. bits). For example (Hill 1973),

$N_{-\infty}$ = $1/P_n$, reciprocal of proportional abundance of the rarest taxon,
N_0 = n, total number of taxa,
N_1 = Exp $[-\Sigma P_i \ln(P_i)]$, exponential of the Shannon–Weaver Index,
N_2 = $1/\Sigma P_i^2$, reciprocal of Simpson's Index,
$N_{+\infty}$ = $1/P_1$, reciprocal of the proportional abundance of the most abundant taxon.

It can be shown that the larger the α, the greater the influence of the most dominant taxa on this effective number; as Hill (1973) states, "The diversity number is figuratively a measure of how many species are present if we examine the sample down to a certain depth among its rarities." For comparative purposes, we have used the partial geometric sequence of N_α with α = 0, 1/4, 1/2, 1,2. This approach provides us with a sliding scale of diversities, from that strongly influenced by the rarest taxa (N_0) to that dominated by the most abundant (N_2).

Clearly N_0 is a measure of species richness. The higher orders of N_α are, however, composite measures of diversity (or heterogeneity as defined by Peet 1974, and Good 1953) and are sensitive to both richness and evenness. Buzas and Gibson (1969) were the first to use N_1/N_0 as a measure of evenness, and Hill (1973) subsequently generalized their approach by considering all possible ratios of his diversity numbers. We have employed here the Hill evenness ratios with N_0 in the denominator because for any α, N_0 is the value of N_α obtained when all the taxa are of equal proportions (i.e. maximum evenness). As before, using different values of α for N_α in the numerator provides a sliding scale, in this case of evenness.

The casual reader might be most interested in examining the relationships obtained for N_0, N_1, and N_1/N_0, as these

TABLE 3. Summary statistics for the linear regression: $N_\alpha = A + B$ ln(biomass) for each N_α and all count sizes. PMC and F refer to the product moment correlation and F-statistic of the linear regression, respectively. RAC and SIG refer to the Kendall rank correlation and its significance, respectively. $^{***}P \leq 0.001$. $^{*}P \leq 0.10$.

Count size		Statistics						Count size	Statistics					
		A	B	PMC	F	RAC	SIG		A	B	PMC	F	RAC	SIG
200	N_0	37.0	−1.48	−0.139	2.57	−0.098	0.048	400	41.7	−1.26	−0.091	1.00	−0.087	0.077
	$N_{1/2}$	32.1	−2.44	−0.403	*** 25.4	−0.238	0.0		38.7	−3.06	−0.405	*** 23.6	−0.259	0.0
	N_1	27.8	−2.50	−0.531	*** 51.3	−0.338	0.0		33.9	−3.21	−0.551	*** 52.4	−0.362	0.0
	N_2	21.5	−2.08	−0.584	*** 67.7	−0.387	0.0		25.7	−2.60	−0.599	*** 67.3	−0.422	0.0
800	N_0	52.3	−2.03	−0.129	1.45	−0.132	0.034	1600	75.5	−4.45	−0.266	* 3.44	−0.262	0.005
	$N_{1/2}$	50.1	−4.38	−0.468	*** 24.2	−0.363	0.0		65.8	−6.34	−0.619	*** 28.0	−0.493	0.0
	N_1	43.0	−4.33	−0.597	*** 47.5	−0.444	0.0		52.5	−5.58	−0.727	*** 50.4	−0.576	0.0
	N_2	31.2	−3.28	−0.629	*** 56.2	−0.466	0.0		34.8	−3.80	−0.744	*** 55.6	−0.578	0.0

statistics have been the most commonly used in previous studies.

DIVERSITY STATISTICS: CALCULATIONS

We have found that to compare the diversity of samples of different count size, a rarefication procedure in which all samples are normalized to some standard count size is necessary (see results; Sanders 1968; Hurlburt 1971; Kempton 1979). This procedure also provides an operational definition of the community under consideration (e.g. the community consisting of the first 800 randomly selected individuals) which is useful when community boundaries are poorly defined, as in the case of large heterogeneous bodies of water.

To evaluate the effect of different count sizes on the predictive equations, we rarefied each sample to standard community sizes of 200, 400, 800, or 1600, the number of rarefications possible depending upon the effective count size of the sample.[2] A total of 47 samples could be rarefied to a count size of 1600, 88 samples to a count size of 800, 122 samples to a count size of 400, and 133 samples to a count size of 200. To implement the rarefication procedure we used an International Mathematical and Statistical Libraries (IMSL) uniformly distributed, pseudo-random number generator to select the appropriate number of individuals without replacement from each sample. The diversity numbers were then calculated for this subsample and another random subsample of the same count size was obtained. This procedure was repeated until a minimum of three and a maximum of 30 subsamples were selected and the diversity statistics calculated. Subsample selection was terminated when the standard error was less than 3% of the mean, over all the diversity numbers (excluding N_0, but see below), or 30 subsamples had been selected. Only rarely was the upper limit of 30 reached.

The exact estimate of N_0 was also calculated for a wide range of samples and rarefied count sizes using the usual formula for sampling without replacement (Hurlburt 1971; Smith and Grassle 1977). The product−moment correlation between the two methods of calculating N_0 was greater than 0.99. N_0, as reported in this paper, was derived from the random subsample method described above. Unfortunately, there are no exact estimates of the higher-order diversity numbers available, making the random subsample procedure necessary.

The relationship between the diversity numbers, evenness, and ln (biomass) was examined using linear regression and the associated product−moment correlation (R), which measures the degree of linear association between two variables (Draper and Smith 1966). The Kendall rank correlation, which makes no assumptions about the form of the functional relationship between two variables (Kendall 1975), is also reported.

[2] As different volumes of a given sample were often examined for taxa of different abundances by varying the number of strips counted, or the magnification used, we took the largest volume enumerated in each sample as a reference and corrected all counts based on lesser volumes upward to this volume. As every countable organism in the largest volume was examined and identified, whether or not it was actually counted, this "effective" count could be justifiably used in the subsequent rarefication procedure.

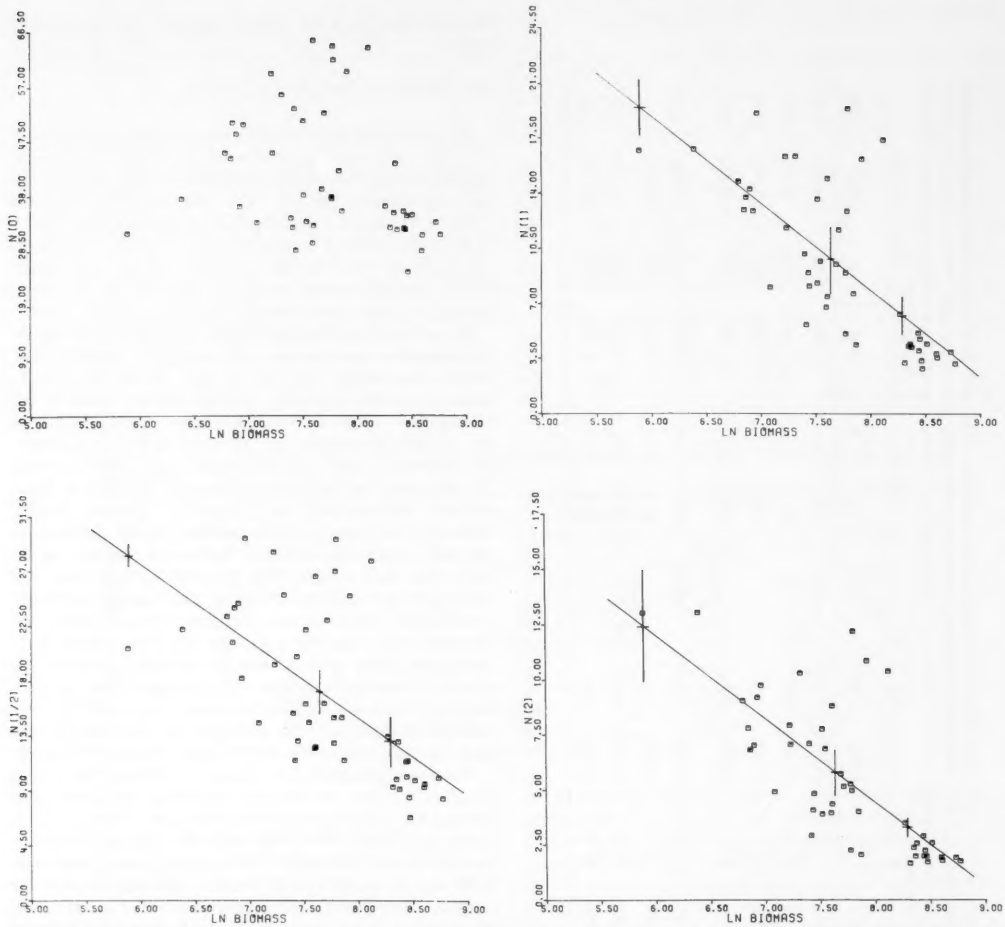

FIG 2. Scatter plots of the four diversity numbers (N_0–N_2) against ln (biomass) for the count size of 1600. Table 3 provides the statistics for the linear regression drawn in. The bars represent 95% confidence intervals for counting error at three levels of biomass.

Our analysis was based on only those 136 out of 163 taxa that were recognizable under low power (225×). We also excluded colorless and benthic species which were occasionally found in the plankton. We have obtained results similar to those reported here by including the 27 taxa countable only under high power. Two independent rarefications must be performed, however, because the low- and high-power counts are independent. As the choice of the ratio between low- and high-power rarefied count sizes is entirely arbitrary, the results are of limited application and we have not pursued the analysis in depth. The importance of normalizing all counts to a fixed count size has dictated this decision; however, as the larger species represent a functionally distinct group relatively secure from zooplankton predation when compared to the smaller species (Gliwicz 1977; Porter 1977), a biological justification exists as well.

Results

Of the 136 taxa used in this analysis, the Chlorophyta was clearly the largest group with 62 taxa, followed by the Bacillariophyta (26 taxa), the Chrysophyta (16 taxa), Cyanophyta (16 taxa), Dinophyceae (6 taxa), Cryptophyceae (6 taxa), and Euglenophyta (4 taxa). A complete list of taxa is available from the authors.

As expected (Hill 1973), the mean number of taxa (N_0) increased with count size (Table 1). Mean biomass also increased with count size, indicating that the higher count sizes tend to come from the more dense samples. The range in biomass was, however, approximately the same for all count sizes. Also as expected, the lower-order diversity numbers (N_0, $N_{1/2}$, N_1) are most sensitive to count size (Table 2), but even N_2 was occasionally sensitive (day 487).

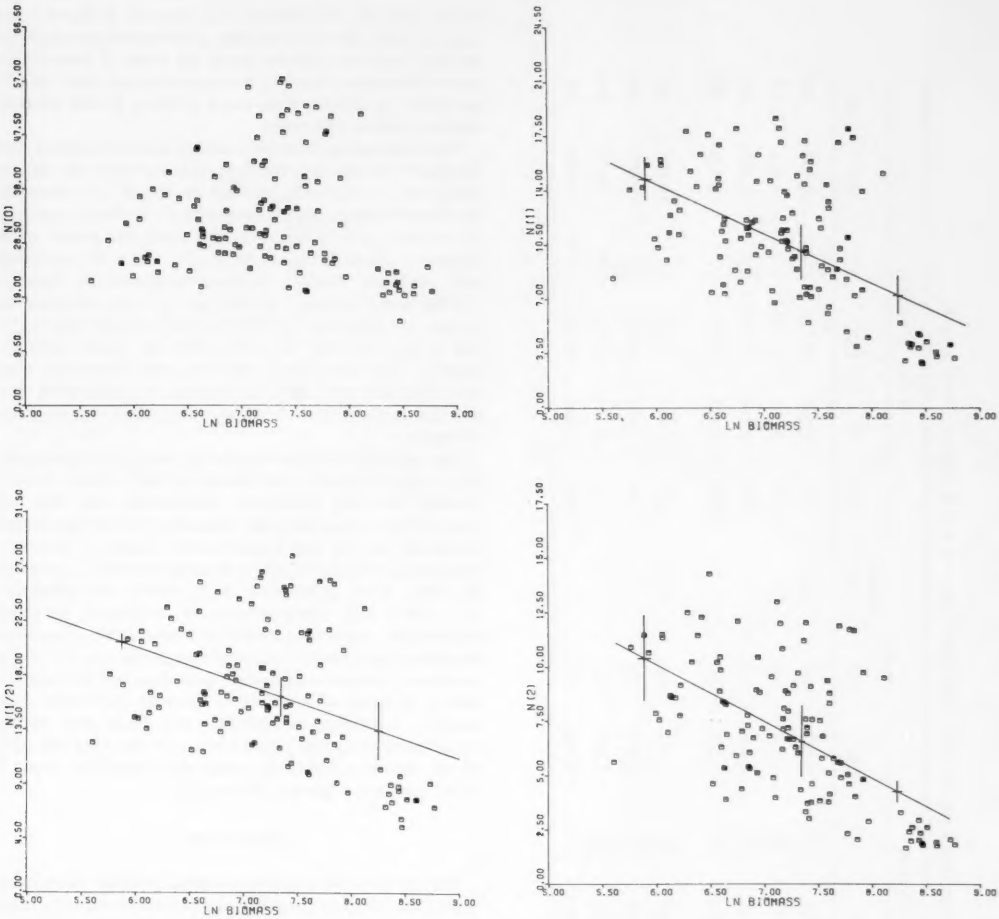

FIG 3. As in Fig. 2, except for the count size of 400. Note that the error bars are based on count sizes greater than 1600 and thus underestimate the variance due to counting in these plots.

Because the measures of evenness are the ratio of a high-order diversity number with N_0, they are invariably sensitive to count size in the range of counts considered here (see also Sheldon 1969; Peet 1975); and, consequently, rarefication was necessary in our analysis.

Three replicate subsamples were enumerated from each of three samples of low, medium, and high levels of biomass to obtain an estimate of counting variability. The effective count size for these replicates was always greater than 1600. The 95% confidence intervals obtained are indicated in all the figures, although they strictly apply only to that data set for which all samples have an effective count size of 1600 or more. The data sets of lower count size would be expected to have much more variance because of enumeration errors.

N_0 exhibited a triangular distribution with biomass: small values at high and low biomass, both large and small values at intermediate levels of biomass (Table 3; Fig. 2, 3). There was a tendency for significant negative correlations between N_0 and ln (biomass) to be obtained at higher count sizes; however, these were small (the product−moment correlation $R = -0.27$). There was also a seasonal component to the variance in N_0. For the count size of 400, all values of N_0 greater than 38 occurred in late summer, between the end of June and mid-August in 1976 and between the end of July and mid-September 1977. Similar results were obtained for all rarefications. For all higher-diversity numbers ($N_{1/2}, N_1, N_2$), the relationships were very significant ($P < 0.001$) and the slope of the linear regression was negative. Both rank and product−moment correlations improved with count size most likely because of a decrease in enumeration error or because

TABLE 4. Summary statistics for the linear regression: $N_a/N_0 = A + B$ ln (biomass). ***$P \leq 0.001$.

Count size		Statistics						Count size	Statistics					
		A	B	PMC	F	RAC	SIG		A	B	PMC	F	RAC	SIG
200	$N_{1/4}/N_0$	1.09	−0.051	−0.711	*** 134	−0.507	0.0	400	1.12	−0.059	−0.732	*** 139	−0.532	0.0
	$N_{1/2}/N_0$	1.11	−0.078	−0.713	*** 130	−0.505	0.0		1.17	−0.092	−0.770	*** 174	−0.565	0.0
	N_1/N_0	1.05	−0.094	−0.704	*** 129	−0.496	0.0		1.10	−0.106	−0.765	*** 169	−0.555	0.0
	N_2/N_0	0.838	−0.082	−0.670	*** 107	−0.471	0.0		0.851	−0.088	−0.724	*** 132	−0.525	0.0
800	$N_{1/4}/N_0$	1.21	−0.075	−0.819	*** 176	−0.631	0.0	1600	1.23	−0.081	−0.870	*** 141	−0.648	0.0
	$N_{1/2}/N_0$	1.31	−0.113	−0.855	*** 233	−0.666	0.0		1.36	−0.125	−0.904	*** 201	−0.687	0.0
	N_1/N_0	1.21	−0.125	−0.841	*** 208	−0.627	0.0		1.21	−0.128	−0.884	*** 160	−0.639	0.0
	N_2/N_0	0.900	−0.098	−0.789	*** 141	−0.563	0.0		0.845	−0.093	−0.812	*** 87.3	−0.584	0.0

of the restricted distribution of the data set at higher count sizes. As seen from the error bars, a substantial amount of the residual variation could be solely the result of enumeration error. Although all diversity numbers of higher order than N_0 are highly significant, there was a tendency for the relationship to improve with order.

The relationships between evenness and ln (biomass) were examined with diversity numbers other than N_0 in the denominator, but N_0 invariably provided the best fit. It is clear that dividing the higher-order diversity by N_0 to obtain a measure of evenness greatly improves the predictive power of ln (biomass) (Table 4; Fig. 4, 5). $N_{1/2}/N_0$ and N_1/N_0 were both well predicted. Product−moment correlations as large as −0.904 and F-statistics as large as 233 were obtained for $N_{1/2}/N_0$ at a count size of 1600. The fit decreased with $N_{1/4}/N_0$ and N_2/N_0. As was the case with the simple diversity numbers, the correlations improved with increasing count size. This may again reflect a decrease in enumeration error or a shift in the relative distribution of samples over the range of biomass.

The distribution of the number of taxa in each taxonomic group suggests that N_0 may be more closely related to some variable reflecting community composition than total biomass. In fact, using only the proportion of the total sample accounted for by the Euglenophyta counts, a product−moment correlation of 0.81 can be achieved with N_0, although all other class proportions were much less predictive ($0.1 < R < 0.5$). Using analysis of covariance, we found that no class proportions contributed substantially (maximum increase of the product−moment correlation was 3%) to the evenness−biomass relationship, indicating that this relationship is of broad applicability in terms of community composition. Under-ice communities and those post ice-out winter samples having a total biomass of less than 100 μg/L do not, however, fall in the predictable range (Fig. 6 and 7) of the evenness−biomass relationship.

Discussion

We conclude that biomass is a good predictor of evenness in the Lake Memphremagog phytoplankton over a wide range of community composition, provided that the counts are rarefied to a fixed and ideally large count size ($0.7 < R < 0.9$). Under-ice and the extremely low biomass communities that occur immediately after ice-out are exceptions.

Species richness cannot be adequately predicted from biomass alone ($0.1 < R < 0.3$), but high richness does occur only at intermediate levels of biomass. Species richness appears to be more directly related to community composition which in turn is related to seasonality, and to a certain extent may reflect differences in the taxonomy of the different algal groups in the phytoplankton.

We can also conclude that composite measures of diversity are predictable from biomass, given the restrictions noted above. The prediction is better than that for richness but poor ($0.4 < R < 0.6$) when compared to evenness.

Hurlburt (1971) noted that: "gradients can exist along which *increases* in species diversity are accompanied by *decreases* in species richness." We have provided here an example of a gradient (total biomass) over which there is no

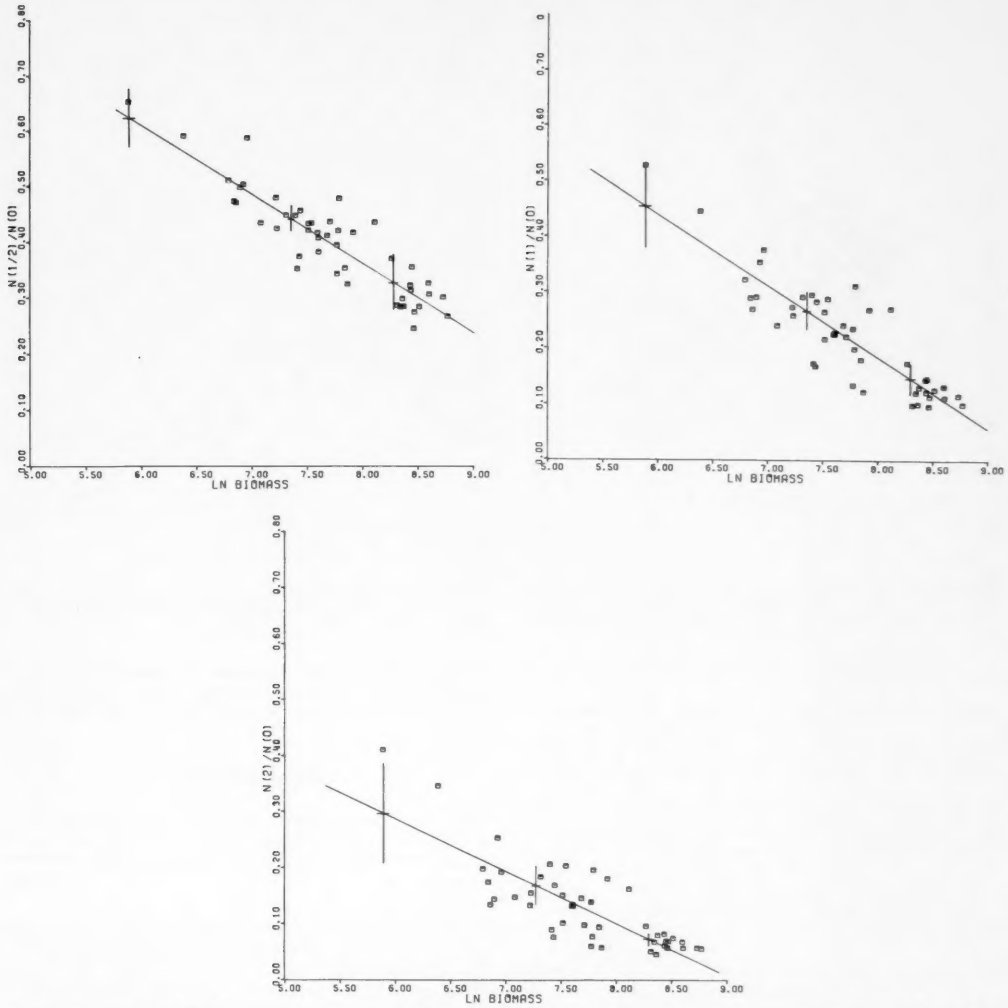

FIG 4. Scatter plots of the three evenness ratios against ln (biomass) for the count size of 1600. Table 5 provides the statistics for the linear regressions that are drawn in. The bars represent 95% confidence intervals for counting error at three levels of biomass.

change in richness but a decrease in evenness. We regard this as further evidence that "diversity" is more predictable when examined as its two component parts: richness and evenness (Odum 1969). Our results confirm Margalef's (1968) prediction that diversity (as measured by the Shannon–Weaver index) should decrease with increasing biomass, but we also show that it is the evenness component of diversity, but not necessarily the richness component, that decreases. More generally, we can conclude that at least one aspect of phytoplankton community structure, the evenness component, is predictable independent of changes in taxonomic composition; and, in particular, it is predicted by the total biomass of the phytoplankton community.

The analysis presented here generates several questions that we are at present unable to answer. We do not know, for example, what factor(s) constrain the relationship between evenness and biomass to be insensitive to changes in community composition. We do not know why under-ice communities present such extreme exceptions to the rule; and we do not know why the Euglenophyta should be such relatively good indicators of species-rich communities. Several hypotheses can be generated to answer these questions. We feel, however, that it is first necessary to expand this investigation to other temperate and tropical lakes to test its generality.

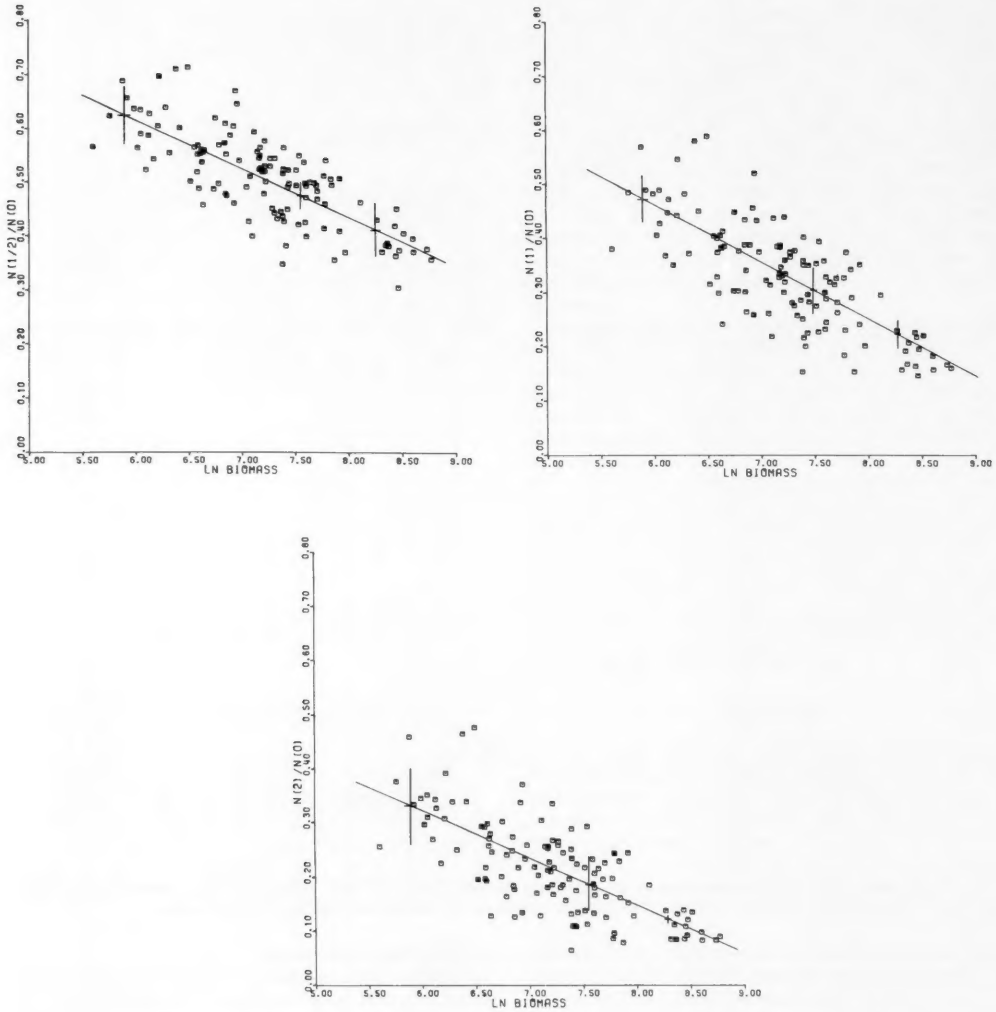

FIG. 5. As in Fig. 4, except for the count size of 400. Note that the error bars are based on count sizes greater than 1600 and thus underestimate the variance due to counting in these plots.

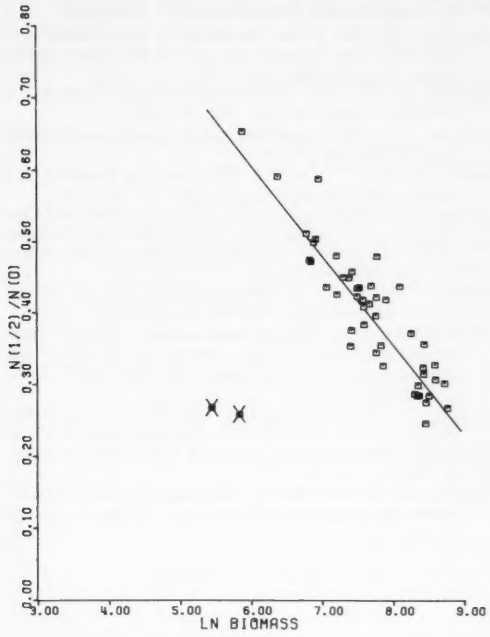

FIG. 6. Two examples of communities which are either under-ice or under 100 μg/L total biomass for count sizes of 1600. The outliers are indicated by large X's. The remainder of the plots are as in Fig. 2.

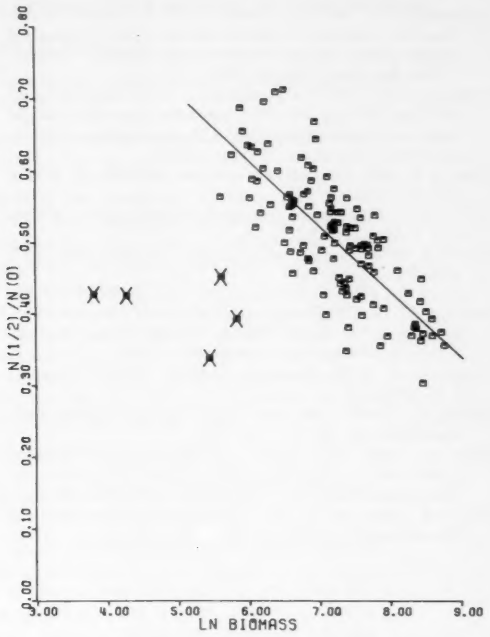

FIG. 7. As in Fig. 6 except for the count size of 400.

Acknowledgments

We thank the whole of the Lake Memphremagog Project, Limnology Research Group for their constructive criticisms of this manuscript. Bill Leggett and Edward McCauley were especially helpful.

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Kinetic Properties of Digestive Carbohydrases and Proteases of Zooplankton[1]

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MAYZAUD, P., AND O. MAYZAUD. 1981. Kinetic properties of digestive carbohydrases and proteases of zooplankton. Can. J. Fish. Aquat. Sci. 38: 535–543.

Copepod carbohydrases and proteases obtained from acetone-dried powder were tested for the effects of various physical–chemical factors. Influences of pH, temperature, substrate concentration, and time of incubation were studied to establish the optimal enzyme assay conditions. Enzyme activities were found that catabolyzed most sugars assayed (amylose, laminarin, cellulose, maltose, cellobiose, lactose, trehalose, α-mannoside, etc.) as well as those catabolyzing most proteins (hemoglobin, albumin, azocoll, cowhide azur). The spectrum of digestive enzymes found is discussed in terms of natural substrate availability. Certain enzymes, such as mannosidase or the chitobiases could be related to the bacterial component in the copepod intestinal flora or diet. From direct and indirect evidences it was possible partially to identify the amylase as an α-amylase, the acid protease as a cathepsin-like enzyme, and one of the alkaline proteases as a trypsin-like enzyme.

Key words: kinetic properties, carbohydrases, proteases, zooplankton

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L'influence des divers facteurs physico–chimiques a été étudiée sur les glycosidases et protéases de copépodes obtenus à partir d'extrait acétonique. Les effets du pH, de la température, de la concentration en substrat et de la durée d'incubation ont été déterminés afin d'établir les conditions optimales des essais enzymatiques. Une activité a été observée pour la plupart des sucres utilisés comme substrats (amylase, laminarine, cellulose, maltose, cellobiose, lactose, trehalose, α-mannoside) et la plupart des protéines (albumine, hémoglobine) ou protéines-substituées (azocoll, cowhide azur). Le spectre d'enzymes digestifs trouvé est analysé en terme de l'existence des substrats in situ. Certains enzymes tels que la mannosidase ou la chitobiase pourraient être liés à la composante bactérienne de la flore intestinale ou de la nourriture. Deux groupes d'enzymes ont été partiellement identifiés: l'amylase s'avère être une α-amylase, la protéase acide un enzyme de type cathepsine et la protéase alcaline un enzyme de type trypsine.

Received June 4, 1980
Accepted January 14, 1981

Reçu le 4 juin 1980
Accepté le 14 janvier 1981

THE marine particulate matter available to planktonic grazers (i.e. copepods) is mainly composed of proteins, carbohydrates, and lipids. The relative proportions of the first two vary with geographical location and time, but they are always more abundant than the third (Mayzaud and Martin 1975). Thus, to obtain a high level of assimilation efficiency, grazers must be well equipped with digestive carbohydrases and proteases. Lipases are, of course, necessary,but they are likely to play a less-important role in energy-gathering processes.

Increased interest in digestive enzymes of marine invertebrates over the past few years has resulted in a large number of papers (see reviews by Van Weel 1970; Bernard 1973), but with the exception of work on *Calanus finmarchicus* by Bond (1934) and Hassler (1937), measurements of amylase and protease activities from various zooplankters from the Mauritanian upwelling by Boucher and Samain (1974, 1975), and on various carbohydrase and protease activities for neritic copepods by Mayzaud and Conover (1976), the zooplankton has been little studied. Although there is extensive literature on kinetic properties of digestive enzymes from decapods (see Van Weel 1970), hardly any information on pH optima and reaction kinetics is available for planktonic Crustacea. To fill this gap, variation in copepod enzyme activity with time of incubation, temperature, pH, and substrate concentration were first investigated to establish optimal enzyme assay conditions, reported here. Various substrates were exposed to the copepod enzyme preparation to estimate its spectrum of activity and, if possible, to relate it to what is known of the biochemistry of marine particulate matter.

Materials and Methods

The animals used in this study were unsorted neritic copepods from the Bedford Basin (Nova Scotia, Canada). A

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Printed in Canada (J6109)
Imprimé au Canada (J6109)

description of the basin can be found in Conover and Mayzaud (1976). The sample used for this study was composed of 50% *Acartia hudsonica*, 20% *Eurytemora herdmanii*, 10% *Oithona similis*, and 10% *Podon* sp. The methodology used for animal collection and enzyme powder preparation is fully described in Mayzaud (1980).

Substrates

All substrates were of high-purity grade. If contaminants were present their relative concentrations were taken into account in activity calculations. Amylose was purchased from BDH (British Drug House, Montreal); Laminarin from ICN (International Chemical and Nuclear Corp.); chitin, maltose, trehalose, methyl-α-glucose, cellobiose, raffinose, melibiose, lactose, azocoll, and cowhide powder azur were purchased from Calbiochem; carboxymethylcellulose, sucrose, salicin, arbutin, albumin, *p*-dinitrophenyl α-D-glucopyranoside, *p*-dinitrophenyl β-D-glucopyranoside, *p*-dinitrophenyl α-D-galactopyranoside, *p*-dinitrophenyl β-D-galactopyranoside, *p*-dinitrophenyl β-D-glucosaminide, *p*-dinitrophenyl β-D-galactosaminide, TAME (*p*-toluene-sulfonyl-L-arginine methyl ester), and BTEE (benzoyl-L-tyrosine ethyl ester) were purchased from Sigma.

Enzyme Assay

Enzyme assay conditions are described in Mayzaud (1980). Modifications were made whenever the routine procedure was not suitable for the experiment, i.e. amylase kinetics were studied using the method of Bernfeld (1951) where enzyme activity is measured by maltose production instead of amylose degradation; carbohydrase activity with *p*-dinitrophenyl derivatives was assayed according to Pollock (1961); and trypsin-like activity and chymotrypsin-like activity were assayed with TAME and BTEE, respectively, according to Hummel (1959). Other modifications will be discussed in the results section.

Results and Discussion

The effects of four different physical–chemical factors on neritic copepod digestive enzymes were tested. These factors were pH, temperature, substrate, substrate concentration, and time of incubation. In the case of amylase, activation by chloride ions was also investigated.

pH

pH kinetics for carbohydrases were assayed with 0.1 mol/L citrate–phosphate buffer adjusted between 4.0 and 8.0. The influence of the ionic composition and molar mass of the buffer was tested with amylase and, contrary to the results of Newcomer (1956), no difference in amylase activity could be detected among citrate–phosphate, phosphate, or acetate buffer (Fig. 1). Identical results on amylase were obtained with the buffer molar mass at 0.02 mol/L and at 0.1 mol/L. As indicated in Fig. 1, most pH optima lay between 4.0 (for α-galactosidase) and 6.0 (for amylase), which is in good agreement with data reported by Van Weel (1970) for various

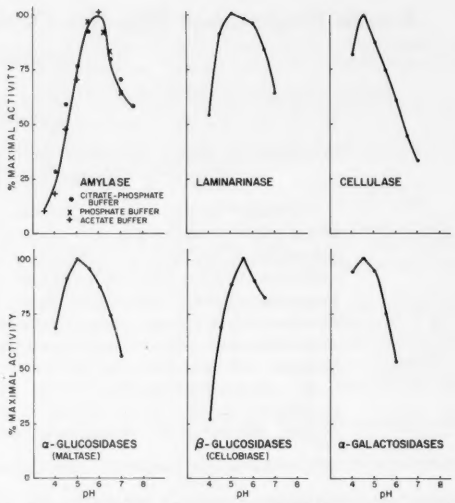

FIG. 1. pH profiles of copepod carbohydrase. The amylase profile was obtained using three different buffers at the 0.02 mol/L concentration. Other profiles were obtained using 0.1 mol/L citrate–phosphate buffer.

Crustacea, although our amylase optimum is somewhat lower than the 7.2 reported by Bond (1934) specifically for the copepod *Calanus finmarchicus* and the 6.8 given by Boucher and Samain (1974) for different species of zooplankton. The discrepancy might be related to differences in buffer, assay temperature (Dixon and Webb 1964), or extraction procedure (Mansour-Beck 1932). Although no value for cellulase pH optimum has previously been reported for Crustacea (Van Weel 1970) or any other zooplankter, our value of 4.5 fits very well with those reported by Stevens (1955) for various yeasts and invertebrates.

The assay of protease pH kinetics used 0.1 mol/L McIlvaine universal buffer (citrate–phosphate system) in the range of 2.5–7.5, and 0.1 mol/L boric acid–sodium hydroxide in the range of 8–11. Four different substrates were used, two natural ones (hemoglobin and albumin) and two synthetic ones (azocoll and hide powder azur). Figure 2 indicates that at least two proteases are present in the glycerol extract, each with a degree of specificity for one of the substrates. Proteases are not usually considered to be substrate-specific but rather act specifically with certain peptide bonds. Our results confirm those of Nilsson and Fänge (1970) on cyclostome proteases; that is, acid protease acted mainly on hemoglobin whereas alkaline acted on albumin.

More puzzling is the kinetics picture obtained with the synthetic substrates (Fig. 2). In both cases, hardly any acidic protease activity could be detected, whereas a broad peak of neutral and alkaline activity was measured between 6.0 and 10.0.

Optimal pH of the digestive enzymes is often compared with the optimal pH for digestion. The pH of the digestive juice of most Crustacea varies between 5.0 and 7.5 (Van Weel 1970) and, though no data are available, probably the values

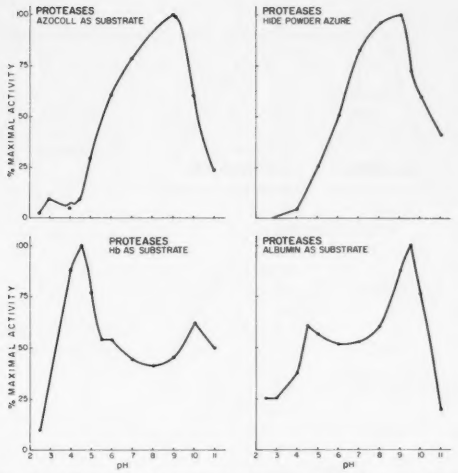

FIG. 2. pH profiles for copepod proteases acting on four different substrates.

for copepods falls within this range. If so, most carbohydrases are close to their optimal pH conditions in the gut, whereas proteases are at less than 50% of their maximum activity. As indicated by Brockerhoff et al. (1970), the discrepancy between enzymatic optima and gastric pH is difficult to explain. It has been suggested that most of the digestion takes place within lumps of food at a pH which may be different from that of the digestive fluid, an explanation which seems inadequate for small animals that shred their food during ingestion as do copepods. Also, in situ pH optima of the digestive enzymes may be different from those measured in vitro. To quote Dixon and Webb (1964), "the effect of pH in enzymes is due to changes in the state of ionization of the components of the system as the pH changes." Digestive juices are known to contain various amounts of protein, polysaccharides, emulsifiers, ions, etc. (Mansour-Beck 1954; Brockerhoff et al. 1970; Van Weel 1970; Pandian 1975) which are not present in the assay medium, but which might affect the operational pH of the enzymes. Moreover, most assays are performed with a crude extract, and the pH optimum of an enzyme also seems to be related to its state of purity (Mansour-Beck 1932).

TEMPERATURE

The influence of temperature on each enzyme was assayed over the range 1–65°C. Depending on the enzyme, the reaction time varied from 10 to 30 min at the pH optima for buffer concentration 0.1 mol/L. The plot of the initial velocity (V), as a percentage of the maximum activity, versus temperature (Fig. 3) generally shows a typical profile for an enzyme-catalyzed reaction. An initial exponential increase of the velocity with temperature up to a "temperature optimum" was followed by a rather sharp decrease, presumably related to heat denaturation. Temperature "optima" (Fig. 3) ranged between 30°C for amylase and 60°C for cellobiase, but as indicated by Dixon and Webb (1964), they are not constant but related to the incubation time adopted in the experimental procedure. As a general rule "optimal" temperature of a given enzyme appears to decrease as the incubation time increases.

Energy of activation (E_A) for each of the enzymes studied was calculated by a least squares fit of log V versus $1/T$ ($°K^{-1}$), using only those values of V corresponding to the exponential range of temperature increase. Similarly, the plot of log V versus t (°C) was used for the determination of Q_{10}. Temperature coefficients presented in Table 1 are well within the range found for other invertebrate digestive enzymes (Evans and Payne 1964; Greenwood and Milne 1968; Morgan 1975) and bracket the values obtained by Packard et al. (1975) for the electron transport system (ETS) in marine plankton. In two cases, laminarinase and cellobiase, a single straight line was not obtained by plotting the log V against $1/T$ but rather two straight lines meeting at an angle. Such a break in slope has been well documented previously (Dixon and Webb 1964) and different interpretations have been given. That it might be related to the occurrence of two forms of the enzyme with different activation energies is plausible, but remains to be shown.

SUBSTRATE CONCENTRATION

Digestion of increasing concentrations of substrate (S) was carried out under optimal pH and temperature conditions defined above. A range of concentrations was prepared by serial dilutions of a stock solution (usually 2%).

Substrate–velocity curves followed Michaelis–Menten kinetics. The calculation of the kinetic parameters (K_m and V_m) was carried out initially using either (1) the least squares fit hyperbola method of Cleland (1967), or (2) the transformation of the Michaelis–Menten equation advocated by Eadie (1942), where the K_m and V_m are computed by plotting V against V/S. As shown by Morgan (1975) the methods give similar values, so the method of Cleland was generally used because of its simplicity and its statistical basis. The values of K_m reported in Table 2 fit fairly well those reported by Evans and Payne (1964), Morgan (1975), and Buonocore et al. (1976) for digestive enzymes of various invertebrates. Amylase K_m is almost the same for zoological groups as different as copepods (1.77 mg/mL, present study), insects (1.80 mg/mL, Buonocore et al. 1976), and crabs (2.22 mg/mL, Blandamer and Beechey 1966). However, K_m found for copepod extracts obtained at different times of the year appeared to vary slightly but significantly ($P < 0.05$) in relation to the biochemical composition of the food supply (Mayzaud and Conover 1976; Mayzaud and Poulet 1978). Since we used crude extracts rather than purified enzymes, it should be useful in future studies to determine whether there are seasonal modifications of enzyme-substrate affinities, or whether any such differences are related to changes in species composition or other factors.

TIME OF INCUBATION

Measurement of enzyme activity is based on the determination of the initial velocity of the enzymatic reaction. Figure 4

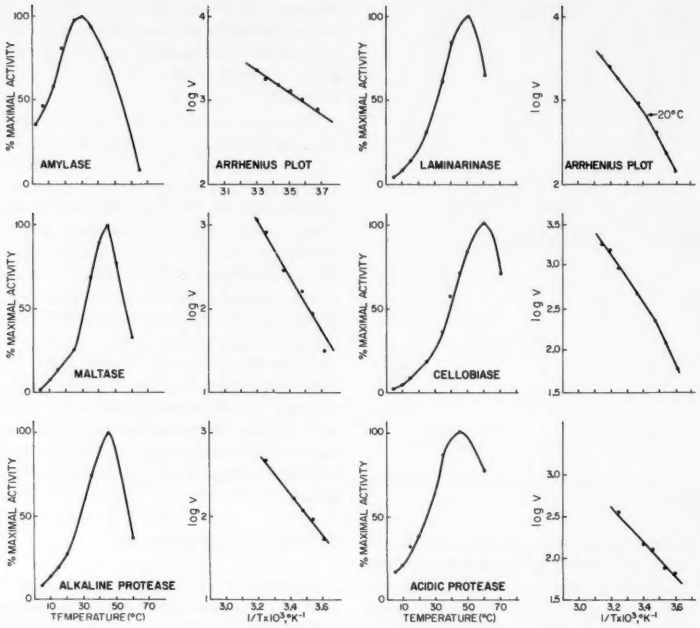

FIG. 3. Temperature profiles and logarithmic plots for the temperature coefficients for various copepod carbohydrases and proteases.

TABLE 1. Temperature coefficients for some of the copepod digestive enzymes.

Enzyme	Energy of activation E_A, cal/mol[a]	Q_{10}
Amylase	8.76	1.31
Laminarinase	10.72−17.10	2.09
Maltase	14.91	2.22
Cellobiase	12.75−20.02	2.05
Alkaline protease	12.00	1.97
Acidic protease	9.94	1.66

[a]1 cal/mol = 4.18 J/mol.

shows that for most enzymes studied, the activity was proportional to the time of incubation up to 45 min. As a general rule, to obtain values as close to the initial velocity, time was kept to the minimum compatible with a significant change in the color reaction used in the assay : 15 min for most carbohydrases and 30 min for proteases.

AMYLASE ACTIVATION BY CHLORIDE IONS

The α-amylase is known to be activated by chloride ions, although not completely inactive in their absence (Greenwood and Milne 1968). In the present experiment, a glycerol extract of the acetone powder was dialyzed overnight at 0°C against distilled water to remove any significant amount of the chloride ions. The dialyzed extract was then used to digest amylose substrate containing increasing amount of sodium chloride. As indicated in Fig. 5, optimal activation took place between 0.01 and 0.1 mol/L. The activity of the dialyzed extract without addition of chloride ions (not shown in Fig. 6) was only 18% of the maximum activity.

ACTIVITY OF COPEPOD DIGESTIVE ENZYMES ON DIFFERENT SUBSTRATES

The extent that neritic copepods can utilize particulate organic matter depends on how efficiently enzymes degrade such organic matter into assimilable molecules. Twenty-seven commercially available substrates for carbohydrases and proteases were assayed with the same crude powder extract. As shown in Table 2, most polysaccharides, di- or tri-saccharides, and proteins were hydrolyzed. As already noted by Mayzaud and Conover (1976), the occurrence of a strong amylase remains puzzling, since $\beta(1-3)$ polysaccharides, rather than starch, predominate in the sea (Handa and Tominaga 1969). Large numbers of starch grains were observed by Bursa (1968) in the Arctic Ocean but this result was never confirmed for the other oceanic area. The strong activity on 1,3-linked glucans (laminarin) was in agreement with the wide distribution of this polysaccharide in the ocean (Handa and Tominaga 1969; Handa et al. 1972). The minor activity against carboxymethyl cellulose was expected, since *Acartia* do not have much cellulase activity (Mayzaud and Conover 1976), and because acetone extraction partially inactivates it (Mayzaud 1980). Whether the poor chitinase activity is real or related to the same technical problem remains to be

TABLE 2. Kinetic constants of some copepod digestive enzymes.

Enzyme	Substrate used	Optimal pH	Optimal temperature °C	Michaelis constant mg/mL ± SE K_m	Energy of activation E_A, cal/mol[a]
Polysaccharidases	Amylose [D-Gluc $\alpha(1-4)$Gluc]$_n$	6.0	30	1.77±0.32	8.76
	Laminarin [D-Gluc $\beta(1-3)$Gluc]$_n$	5.0	50	0.37±0.07	14.33
	Carboxymethylcellulose [D-Gluc $\beta(1-4)$Gluc]$_n$	4.5	50	6.16±0.08	19.22
	Chitin [AcGluc $\beta(1-4)$AcGluc]$_n$	ND	—	—	—
Di-trisaccharidases α-Glucosidases	Maltose [D-Gluc $\alpha(1-4)$Gluc]	5.0	45	0.75±0.04	14.91
	Sucrose [D-Gluc $\alpha(1-2)$-DFruct]	ND	—	—	—
	Trehalose [D-Gluc $\alpha(1-1)$Gluc]	6.0	45	0.53±0.05	21.58
	p-Dinitrophenyl α-D glucopyranoside	5.0	—	—	—
β-Glucosidase	Cellobiose [D-Gluc $\beta(1-4)$Gluc]	5.5	60	0.36±0.05	15.11
	Salicin [β-D-Gluc and Saligenin]	ND	—	—	—
	Arbutin [β-D-Gluc and Hydroquinone]	ND	—	—	—
	p-Dinitrophenyl β-D glucopyranoside	5.5	—	—	—
α-Galactosidase	Raffinose [Gal$\alpha(1-6)$Gluc$\alpha(3-2)\beta$Fruct]	ND	—	—	—
	Melibiose [Gal$\alpha(1-6)$ βGluc]	ND	—	—	—
	p-Dinitrophenyl-α-D galactopyranoside	4.0	—	—	—
β-Galactosidase	Lactose [Gal-$\beta(1-4)$Gluc]	5.0	60	24.49±0.79	21.79
	p-Dinitrophenyl-β-D galactopyranoside	5.0	—	—	—
Other Saccharidases					
α-Mannosidase	*p*-Dinitrophenyl-α-D-mannoside	5.0	—	—	—
N-acetyl glucosaminidase	*p*-Dinitrophenyl-β-D-acetyl glucosaminide	5.0	—	—	—
N-acetyl galactosaminidase	*p*-Dinitrophenyl-β-D-acetyl galactosaminide	6.0	—	—	—
Proteases					
Acidic	Hemoglobin	4.5	45	0.17±0.01	9.94
Alkaline	Albumin	9.5	45	0.79±0.10	12.26
Alkaline	Azocoll	9.0	—	—	—
Alkaline	Hide-powder azur	9.0	—	—	—
Trypsin-like	TAME	9.0	—	—	—
Chymotrypsin-like	BTEE	ND	—	—	—

[a]1 cal/mol = 4.18 J/mol.

shown. However, chitin is quantitatively a minor component of the natural particulate matter and a strong chitinase would be of little benefit to filter-feeding copepods.

Of the four α-glucosides tested, only sucrose was not hydrolyzed. The large maltase activity was expected because of the strong amylase observed, since α-amylase hydrolysis of starch leads to maltose residues which have to be split to glucose before assimilation (Pandian 1975). Trehalase activity was minor and probably related to the occurrence of trehalose in certain algae, fungi, and bacteria (Elbein 1974). The

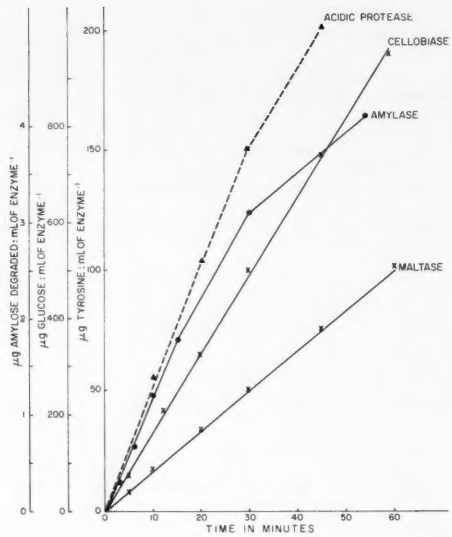

FIG. 4. Effect of incubation time for copepod amylase, maltase, cellobiase, and acidic protease for the same acetone powder concentration.

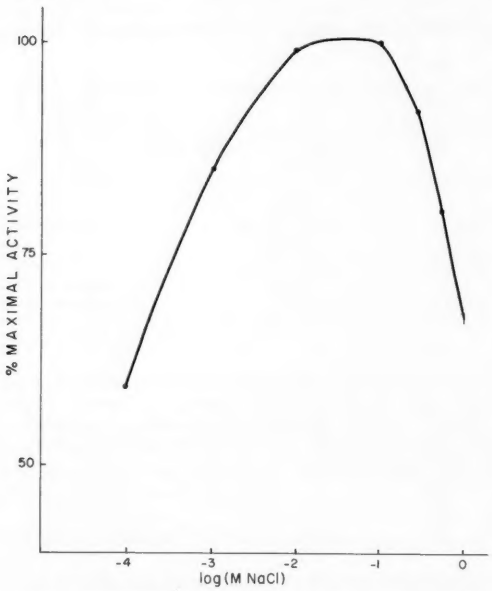

FIG. 5. Activation of copepod amylase activity by sodium chloride.

β-glucosides, such as cellobiose or *p*-dinitrophenyl β-D-glucopyranosides, appeared to be readily hydrolyzed. Cellobiase activity has been reported for almost all invertebrates (Van Weel 1970; Dadd 1970; Hillenberg 1972), even for those species which do not have significant cellulase activity. Cellobiose is not assimilated as a free sugar, but generally results from the enzymatic degradation of cellulose and lichenin. The nature of the marine substrate used by this enzyme could be glycans connected via β-linkage to an aglycon (Hillenberg 1972), but their natural existence remains to be proven. Another possibility could be that the β-glucosidase detected was in fact a mixture of a cellobiase and a laminarabiase both acting on cellobiose. Laminarabiase is responsible for the hydrolysis of laminarabiose D-glucose β(1,3)glucose, a product of enzymatic degradation of laminarin (Pazur 1970). The theory of two β-glucosidases would help to explain the discontinuity noted in the Arrhenius plot of cellobiase (Fig. 3). Lack of activity with salicin and arbutin indicate that the specificity of the copepod β-glucosidases can discriminate between glucosides containing aglycons, such as saligenin or hydroquinone on one hand, and *p*-dinitrophenyl on the other.

Both α-and β-galactosidases are widely distributed among invertebrates (Van Weel 1970; Hillenberg 1972). In a previous report, Mayzaud and Conover (1976) indicated that no α-galactosidase could be detected in copepod extract. In the present study, no hydrolysis of either raffinose or melibiose was observed, although later experiments have shown a weak activity against *p*-dinitrophenyl α-D-galactopyranosides. Whether such a weak activity is of any importance for the copepod assimilatory capability is doubtful, as neither raffinose- nor melibiose-type molecules have been reported in the marine environment. The significant activity of a β-galactosidase against substrates such as lactose or *p*-dinitrophenyl β-D-galactopyranoside is also interesting because the occurrence of lactose in the natural diet of zooplankton is not known. It is probable that copepod lactase is in fact a relatively nonspecific β-galactosidase acting on most marine β-galactosides. Various substrates such as the galactolipids of algae are susceptible to hydrolysis by α- and β-galactosidases (Benson and Shibuya 1962).

In addition to the five major classes of carbohydratases, different minor substrates were also tested for possible hydrolysis. The *p*-dinitrophenyl α-D-mannoside was degraded at pH 5 as was *p*-dinitrophenyl-β-D-acetyl glucosaminide. Hydrolysis of *p*-dinitrophenyl β-D-galactosaminide occurred at pH 6. The existence of a mannosidase has been reported in various invertebrates (Snaith and Levy 1973) and appeared to be mainly involved in the degradation of glycoproteins. Beta-glucuronidases are widely distributed among both plants and animals and are essentially involved in the degradation of glucuronids and mucopolysaccharides rich in glucuronic acid. *N*-acetyl glucosaminidase is considered by certain authors as identical with chitobiase (Jeuniaux 1963) and is involved in the hydrolysis of *N*-acetylglucosamine residue coming from the enzymatic degradation of chitin. The lack of chitinase reported here is somewhat contradictory with the significant chitobiase measurement, but *N*-acetyl glucosaminide, as well as *N*-acetyl galactosaminide, are also constituents of glycoproteins and bacterial mucopolysaccharides (Karlson 1964). The occurrence of glucuronidase, *N*-acetyl glucosaminidase, and *N*-acetyl galactosaminidase could also be related to the bacterial component in the copepod diet.

The Nature of Copepod Amylase and Proteases

It is usually assumed that animal amylases are of the α-type, yielding maltose in an α-configuration. During hydrolysis they quickly destroy the iodine reaction with starch to yield low molecular weight dextrins and finally maltose. Alpha-amylases are able to attack strongly branched polysaccharides such as starch, amylose, amylopectin, and glycogen. Beta-amylases, on the other hand, yield maltose in the β-anomeric form and a high molecular weight dextrin that usually still has the iodine reaction. Degradation of starch by copepod amylase was followed through time and the typical five-color steps (Somogyi 1940) of α-amylase were obtained. Activation of copepod amylase by chloride ions is also indicative of α-amylase, since β-amylase is not known to require either coenzymes or metals for maximum activity. We are aware that the present distinction between α- and β-amylase is made in old-fashioned terms and that purification of the amylase would be necessary to study its activity more accurately. Measurements of the optical rotation during the enzyme hydrolysis would be an alternate procedure (Meeuse and Fluegel 1958).

TAME (*p*-toluene-sulfonyl-L-arginine methyl ester) and BTEE (benzoyl-L-tyrosine ethyl ester) are artificial peptides specific for trypsin-like activity and chymotrypsin-like activity, respectively. The complete lack of chymotrypsin activity (Table 1) is not really surprising as very few crustaceans have been shown to have it (Huggins and Munday 1968). On the other hand, the alkaline proteases from copepods, like those of other crustaceans (Van Weel 1970; Huggins and Munday 1968), have the same characteristics as mammalian trypsin.

The nature of the acidic protease was more difficult to ascertain. Its pH optimum of 4.5 rules out a pepsin-like response, for which the optimum is rarely higher than 3.5 (Barrington 1962). Possibly we could be dealing with a cathepsin-like enzyme which, according to the classification of mammalian cathepsins by Fruton and Mycek (1956), could be a mixture of cathepsin A and B. Quoting from Nilsson and Fänge (1970) in animals (such as copepods) "lacking pepsin and hydrochloric acid the catheptic activity may be of considerable importance. It is possible that the extracellular enzymes have evolved from tissue enzymes in parallel with morphological development of the digestive tract."

Conclusions

Copepods, like most marine invertebrates, appeared to be well equiped to digest most of the organic compounds known to occur in their potential food supply. The question of whether the enzyme composition and secretion fit the diet has been considered by many authors (Van Weel 1970; Kapoor et al. 1975) and answered positively by some (Van Weel 1961). The separation between herbivorous and carnivorous organisms is usually based on the hypothesis that carbohydratases are essentially secreted by animals feeding on a plant diet whereas proteases correspond to an animal-type diet. The results summarized by Kapoor et al. (1975) for different fishes and by Huggins and Munday (1968) for crustaceans showed that there are numerous exceptions to such a relationship probably because of the differences in physiological states of the test animals and the oversimplified representation of the digestive system made when comparing only amylase and trypsin.

When considering zooplankton, such division is even more difficult since there are almost no strictly herbivorous copepods (Conover 1978). The size of the particulate matter available to them varies from 2 to 150 μm equivalent diameter (Poulet 1973), and in the Bedford Basin this range comprises flagellates, diatoms, dinoflagellates, silicoflagellates, and microzooplankton as well as detritus. Each of these components has a different biochemical composition and their relative abundance varies greatly with time (Mayzaud and Taguchi 1979). Copepods are feeding on both living and nonliving particles (Poulet 1976) and they use different parts of the particle-size spectrum depending on the stage of growth of the species. The nutritional value of such natural diets is difficult to evaluate, as it depends on the degree of digestibility and its content in essential elements, i.e. the nutritional character of the organism considered.

As indicated by Mayzaud and Conover (1976) proteins are the major constituents of most particles and contain most of the so-called essential aminoacids (Cowey and Corner 1963, 1966; Okaichi 1974). As proteases have usually very broad specificities, the exact nature of the ingested protein is probably not critical. Carbohydrates generally stem from the phytoplankton fraction of the particulate matter and have been divided between soluble (inacid or alkali) and insoluble ones (crude fibers) (McAllister et al. 1961; Parsons et al. 1961). Stored reserves vary with the phytoplankton group: diatoms synthesize $\beta(1-3)$polyglucans or chrysolaminarin (Handa and Tominaga 1969) whereas dinoflagellates contain starch-type reserves and structural cellulose. Bursa (1968) has observed in the Arctic many starch granules in sea water during a period of mass mortality of *Gymnodinium* cells, which is probably the reason his observations differ from those of Handa and Tominaga (1969) in different waters. So far as we know there have been no reports of large amounts of chemically defined starch-like molecules in oceanic or temperate neritic waters. A logical choice for an indicator of herbivorous tendencies should be the laminarinase activity, but its specificity remains to be shown. The number of species studied so far is too small to allow us to draw any general conclusions, but it is probable that at least amylase, cellobiase, and lactase activities should be explained in terms of enzyme-substrate relationships. To what extent the study of amylase alone represents the characteristics of the carbohydrate–carbon digestive system remains to be demonstrated, and the work of Boucher and Samain (1976) should be reexamined using a larger spectrum of enzyme activities. The adequacy of the chemical composition of the food supply cannot be evaluated before the nature of the substrate ingested is known and the specificity of enzyme induction verified.

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Discrimination by External Features between Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*)

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This study reviews methods formerly recommended for discriminating between the alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) and suggests an alternate, more efficient, external species-specific character. The method relies on differences in scale imbrication patterns and scale morphology.

Key words: alewife, *Alosa pseudoharengus*; blueback herring, *A. aestivalis*; morphology, meristics, identification

MACLELLAN, P., G. E. NEWSOME, AND P. A. DILL. 1981. Discrimination by external features between alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*). Can. J. Fish. Aquat. Sci. 38: 544–546.

Nous passons en revue, dans l'article qui suit, les méthodes jadis recommandées pour distinguer le gaspareau (*Alosa pseudoharengus*) et l'alose d'été (*A. aestivalis*). Un autre caractère externe particulier à l'espèce, plus sûr, est suggéré. La méthode est fondée sur la configuration de l'imbrication des écailles et sur la morphologie de ces dernières.

Received May 12, 1980
Accepted February 5, 1981

Reçu le 12 mai 1980
Accepté le 5 février 1981

THE "gaspereaux" of the Atlantic coast consist of two closely related clupeid species of anadromous river herrings, alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*). Their ranges overlap almost completely (Bigelow and Schroeder 1953; Scott and Crossman 1973) and their spawning migrations are often into the same drainage systems. The alewife 'run' usually precedes the 'run' of the blueback herring because the latter prefers warmer temperatures (Hildebrand and Schroeder 1928; Scott and Crossman 1973). Because of their remarkable similarity and frequent co-occurrence they are often confused.

Bigelow and Schroeder (1953) and Leim and Scott (1966) present several ways in which the alewife and blueback herring can be identified. Alewives are reported to have a broader eye than snout length, while the bluebacks have an eye diameter that is less than or equal to snout length. It is also suggested that the alewife can be distinguished by its greyish-green back, which differs from the blue-green back of the blueback herring.

The color of the peritoneal lining of the body cavity is perhaps the most useful feature separating the two species, alewives having a pinkish to greyish peritoneum in contrast to the black peritoneum of the blueback herrings (Leim and Scott 1966; Scott and Crossman 1973). Also, Scott and Crossman (1973) note that the shape of the otolith is distinctive for both species, and Price (1978) gives a good description of major differences. McKenzie (1973) has shown that muscle myogen patterns, obtained using electrophoretic techniques, are distinctly different. Chambers et al. (1976) demonstrated that the larvae of the two species differ particularly in regard to the numbers of myomeres, and Messieh (1977) has shown that alewives have fewer vertebrae than blueback herrings. Scott and Crossman (1973) and Messieh (1977) also report other meristic differences between the two species; blueback herring possess fewer dorsal and anal fin rays than the alewife, and bluebacks have more than 45 gill rakers on the lower gill arches whereas alewives possess fewer than 45.

Because of recently increasing commercial interest in these species, fisheries biologists need to know more about the

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Printed in Canada (J6070)
Imprimé au Canada (J6070)

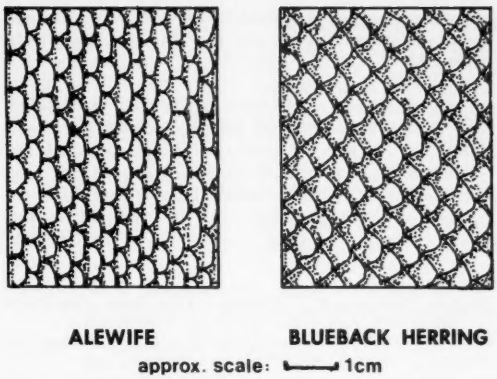

FIG. 1. Diagram of the region between cleithrum and vent below the lateral line, comparing the different scale imbrication patterns of the alewife and blueback herring.

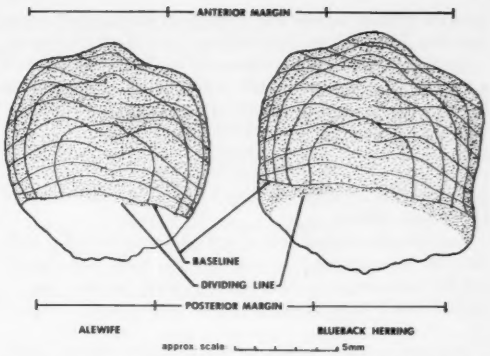

FIG. 2. Diagram comparing scale morphologies of the alewife and blueback herring. Scales obtained from the midline region above the vent.

population dynamics of these stocks to estimate yields and other population statistics. The required data in regard to the populations of anadromous alewives and blueback herrings are difficult to obtain because of frequent misidentifications. Tagging studies are particularly subject to error because external features must be utilized to discriminate between the two species. In this paper the currently used external features applied in the identification of the two species are examined, and an alternate, more efficient, discriminator is recommended.

Materials and methods — A total of 185 alewives and 171 blueback herrings were collected from the West River, Antigonish Co., Nova Scotia, between May 15 and July 3, 1978, using trap nets and seines. Specimens were tagged and frozen for later analysis. Upon thawing, specimens were identified by examining the color of the peritoneum, and in addition to standard body measurements the following data were obtained: eye diameter (nearest millimetre) and snout length (distance between tip of snout and anterior margin of eye orbit, to the nearest millimetre). Two scale samples were removed, from the midline region above the vent of each specimen (Rothschild 1963), cleaned, and mounted dry, between two microscope slides taped together. Random samples of otoliths were also collected from representatives of both species.

In the course of examining the scales of both species a feature was noted which differed markedly between the two species. To test the utility of this feature as a species-specific discriminator, a random set of 30 scales was prepared, taken from 16 blueback herrings and 14 alewives, ranging in ages from II to VII. Ten naive subjects were instructed concerning the species-specific feature and asked to identify the set of prepared scales.

To confirm the usefulness of the above feature and its applicability to other populations, 10 specimens of the two species were collected during the summer of 1979, from each of the following drainage systems; West River, Antigonish Co., the Margaree River, Inverness Co., and the Gaspereau River, Kings Co., Nova Scotia. These specimens were treated and studied as described above.

Results — The color of the peritoneal lining was found to be reliable in species recognition. Otolith samples were similar to those described by Price (1978). No substantial difference was observed in the back color of the two species, which seemed to vary with ambient lighting conditions.

Eye diameter to snout length ratios compared by analysis of variance demonstrated a significant difference ($P < 0.001$) between the two species. However, the means were very close, 1.03 for the alewives and 0.94 for the bluebacks. Although eye orbits are relatively broader in the alewives than the bluebacks, the small difference that does exist limits the usefulness of this feature as a discriminating characteristic.

While studying the samples, a difference was noticed in the scale patterning on the sides of the fish (Fig. 1). Scale edges of the alewife appeared as a 'scallop-like' pattern, while those of the blueback herring produced a more 'diamond-like' pattern. Closer observation revealed a difference in the markings on the scales themselves, which was due to differences in the type of insertion in the scale pocket.

Scales of the alewife and blueback herring are cycloid, large, and distinctly marked. The anterior three-quarters of the scale is striated by transverse grooves and ridges, annuli, and spawning marks (Marcey 1969). In contrast, the posterior portion is transparent. The most posterior transverse groove has been named the baseline by Cating (1953; cited by Rothschild 1963). For the purposes of this study, it was necessary to define a dividing line (Fig. 2) as the margin between the imbedded and exposed portion of the scale (or the anterior and posterior areas).

The method of discriminating between the scales is based on the position of the dividing line in relation to the baseline. In the alewife, the dividing line approximately parallels the baseline, forming a transversely oriented straight line across the scale (Fig. 2). In contrast, the dividing line of the blueback herring describes an arch or an angle of less than 180°. In doubtful cases, examination of the periphery of the scale of bluebacks showed the dividing line to be posteriorly removed from the baseline, which did not occur in the alewives. In a few situations where the dividing line appeared to be removed

from the baseline on one half of the scale and parallel to it on the other, invariably the scale belonged to a blueback herring.

Results of the scale discrimination test administered to 10 naive subjects revealed high precision in distinguishing between the two species. A total of seven errors of identification were made. The errors committed involved two scale samples (one scale was misidentified five times and another twice) (Chi-square test, $P < 0.005$). These results demonstrate that the technique is very reliable over the range of age-classes utilized.

Examination of specimens of both species collected in 1979 from the Margaree and Gaspereau rivers, N.S., also showed that the scales were reliable in distinguishing between the two species within these drainage systems.

Discussion — A number of morphological features have been suggested for distinguishing between the alewife and blueback herring. With the exception of those reported by Scott and Crossman (1973) and Messieh (1977), the snout length versus eye diameter method (Bigelow and Schroeder 1953; Leim and Scott 1966) all require killing the fish. This is of little use for those wishing to identify, mark, and release specimens for future study. In particular, population studies of the two species have been severely hampered by the lack of an efficient method of distinguishing between them.

Comparisons made during this study revealed that although the snout length−eye diameter method (Bigelow and Schroeder 1953; Leim and Scott 1966) is statistically reliable, its usefulness in the field is severely limited because of the very minor differences involved. The method is also cumbersome, requiring anesthesia and undue handling of the specimens. Similarly, features such as counts of the number of gill rakers on the lower gill arch and the number of dorsal and anal fin rays (Scott and Crossman 1973; Messieh 1977) require that specimens be anesthetized and handled excessively.

The scale differences are highly reliable and require a minimum of handling. Simple observation of the scale imbrication pattern is usually sufficient to identify the species. For doubtful cases, examination of a scale with a hand lens is adequate for species recognition. Using this method, large numbers of river herrings can be accurately sorted. However, the reliability of this method for ages less than II remains to be confirmed.

Acknowledgments — We thank Dr Graham Daborn and Mr John O'Neil, Department of Biology, Acadia University, Wolfville, N.S., who provided us with samples of alewife and blueback herrings collected from the Margaree and Gaspereau rivers. The Natural Sciences and Engineering Research Council and the University Council for Research, St. Francis Xavier University, provided financial support for this work.

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Transmission of Bacterial Kidney Disease from Wild to Stocked Hatchery Trout

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MITCHUM, D. L., AND L. E. SHERMAN. 1981. Transmission of bacterial kidney disease from wild to stocked hatchery trout. Can. J. Fish. Aquat. Sci. 38: 547–551.

Natural, horizontal transmission of bacterial kidney disease (BKD) from infected wild brook trout (*Salvelinus fontinalis*) to newly stocked hatchery brook trout, brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) was shown in a small lake and stream system in southeastern Wyoming, USA. Stocked trout were infected naturally and died in 9 mo or less after exposure to infected wild fish. Dead and live fish collected from each of three stations were necropsied. Fluorescent antibody techniques (FAT) were used to detect the BKD organism in all samples. Low severity infections were often detected by FAT at a higher rate when feces were examined as compared to kidney tissues from the same fish. Because other known pathogens were essentially absent, BKD was diagnosed as the cause of all deaths in both stocked hatchery fish and wild fish. Rainbow trout were found to be the most refractory species.

Key words: bacterial kidney disease, natural disease transmission, wild trout, brook trout, brown trout, rainbow trout, epizootics

MITCHUM, D. L., AND L. E. SHERMAN. 1981. Transmission of bacterial kidney disease from wild to stocked hatchery trout. Can. J. Fish. Aquat. Sci. 38: 547–551.

L'article qui suit décrit la façon dont la maladie bactérienne du rein (BKD) a été transmise horizontalement, dans la nature, de stocks sauvages infectés d'ombles de fontaine (*Salvelinus fontinalis*) à des ombles de fontaine, truites brunes (*Salmo trutta*) et truites arc-en-ciel (*Salmo gairdneri*) d'élevage nouvellement ensemencés dans un petit lac et cours d'eau du sud-est du Wyoming (É.-U.). Les truites ensemmencés furent infectées naturellement et moururent en dedans de 9 mois après exposition à des poissons sauvages infectés. Nous avons examiné à l'état mort des poissons qui avaient été recueillis morts ou vivants à chacune des trois stations. Des techniques de fluorescence des anticorps (FAT) ont servi à détecter l'organisme de la BKD dans tous les échantillons. Souvent, les FAT ont détecté des infections peu sévères plus rapidement quand les fèces étaient examinées, comparativement à des tissus rénaux provenant des mêmes poissons. D'autres organismes pathogènes étant virtuellement absents, nous avons conclu que la BKD était la cause de toutes les mortalités, tant des poissons d'élevage ensemencés que des poissons sauvages. La truite arc-en-ciel s'est avérée l'espèce la plus réfractaire.

Received July 28, 1980
Accepted January 19, 1981

Reçu le 28 juillet 1980
Accepté le 19 janvier 1981

BACTERIAL kidney disease (BKD) is an acute to chronic systemic infection of salmonid fish caused by *Renibacterium salmoninarum* (Sanders and Fryer 1980), and that occurs over a wide range of water temperatures (Bullock et al. 1971; Wood 1974; Sanders et al. 1978; Mitchum et al. 1979). Bacterial kidney disease can cause high mortality in propagated trout and salmon (Ordal and Earp 1956; Allison 1961; Wood 1974; Bullock et al. 1975) and can significantly reduce salt water acclimation, ocean survival, and returns to freshwater of both Pacific salmon (Wood and Wallis 1955) and Atlantic salmon (*Salmo salar*) (Smith 1964; Frantsi et al. 1975, 1977). Attempts to cure the disease by chemotherapy have been unsuccessful (Snieszko and Griffin 1955; Wolf and Dunbar 1959a; Warren 1963a).

Printed in Canada (J6177)
Imprimé au Canada (J6177)

Although BKD has been reported in a few wild or apparently wild fish populations (Wood and Wallis 1955; Smith 1964; Pippy 1969; MacLean and Yoder 1970; Evelyn et al. 1973; Frantsi et al. 1975; Ellis et al. 1978; Mitchum et al. 1979; Paterson et al. 1979), most records and reports deal with occurrences of the disease in hatcheries where it may be enzootic or infrequent (Warren 1963b; Bullock et al. 1975). Mitchum et al. (1979) conducted an extended study which determined the prevalence and effects of BKD in wild naturally reproducing populations of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) in the French Creek–Brush Creek drainage system in southeastern Wyoming, USA, where annual BKD epizootics occurred. The source of the disease is thought to have been infected hatchery trout stocked into the stream from a station with a history of BKD and the only hatchery ever to have provided fish for the creek. The suspect fish had been

stocked 13 yr or more before the study was initiated. The purpose of this study was to determine if BKD would be transmitted from infected wild trout in a small lake and stream system to newly stocked hatchery salmonids, and if transmission occurred, to determine the relative susceptibility of different species to the disease.

Materials and methods — Three fish stocking and sampling stations were established on the headwaters of the French Creek–Brush Creek drainage system. The study area includes one 4.8-ha lake (Station 1) and about 6.4 km of upper North French Creek. In an earlier study, this area was determined to be the focus of infection for wild trout in the drainage because of the deaths which occurred there and because of the high incidence and severity of BKD in the fish examined from these stations (Mitchum et al. 1979). Wild brook trout were the only fish species found in the study area, except for two longnose suckers (*Catostomus catostomus*) which were collected at Station 1 (Sucker Lake) in the earlier study.

Hatchery brook trout, brown trout, and rainbow trout were obtained from two state fish culture stations which have a history of being free from BKD and other serious fish diseases. A sample of 60 live fish of each species (Ossiander and Wedemeyer 1973) was examined for BKD and other diseases. After determining that these hatchery fish were negative for BKD, 3000 of each species were marked by removing the right pelvic fin. On September 8, 1976, 1000 of each species were stocked into each of the three study stations. The brook trout averaged ~ 33 fish/kg (140 mm long); the brown trout 56 fish/kg (114 mm long); and the rainbow trout 111 fish/kg (102 mm long). The brook trout and brown trout were 11 mo old, and the rainbow trout were ~ 7 mo of age when stocked. After stocking, each station was checked for dead fish twice a week through mid-October 1976. Four brook trout, six brown trout, and eight rainbow trout were collected during this period. These 18 specimens were necropsied and found to be negative for *R. salmoninarum* and other pathogens. Trauma or stress from stocking was thought to be the cause of death in these hatchery trout.

During the following year, from June 22 to September 30, 1977, checks were made twice a week at each station, and dead fish were collected, except for the period between June 22 and July 16 when, because of poor accessibility, only two collection trips were made. Five additional collections were made at each station during 1978. Also, during 1977 an attempt was made to collect a sample of 60 live hatchery fish of each species with gill nets from Station 1 and with electrofishing gear from each of the other two stations (Ossiander and Wedemeyer 1973). Because an insufficient sample was collected at Station 1 in 1977, this sample was supplemented by collections made in 1978.

The same necropsy and examination procedures (McDaniel 1979), culture methods (Evelyn 1977), severity of BKD infection determination (Lewis and Allison 1971), and microscopic equipment used in the earlier study of wild trout (Mitchum et al. 1979) were used for all collected fish. However, both indirect (Bullock and Stuckey 1975) and direct (Bullock et al. 1980) fluorescent antibody techniques (FAT) were used to identify *R. salmoninarum* isolated in cultures, and to detect the organism in kidney tissue smears, and occasionally, fecal sample smears. During the course of this study the simpler, more efficient, direct FAT (Bullock et al. 1980) became available and was used thereafter. Also, after this study was initiated we found that it was often easier to detect *R. salmoninarum* in fecal samples than in kidney samples. The reason for this phenomenon was not determined. Perhaps it is due to a possibly larger number of BKD bacteria present in fecal samples; or perhaps because of the different nature of kidney tissue versus fecal material. The FAT was used on both kidney tissue smears and fecal sample smears from some collected fish. Detection rates on these samples were compared.

Results and discussion — Bacterial kidney disease was diagnosed in all dead fish collected from the three study stations during 1977 and 1978 (Table 1), showing that BKD was transmitted horizontally from infected wild brook trout to the newly stocked hatchery brook trout, brown trout, and rainbow trout. One dead hatchery rainbow trout was found at Station 1 on June 22, 1977, the first collection trip made to the study area that spring. No dead fish were found at Stations 2 or 3 (North French Creek), but the stream was mostly covered by snow and ice during June. Dead wild trout and all three species of stocked trout were found at each station during the second collection trip on July 16, 1977. The hatchery trout were stocked on September 8, 1976. Therefore, these fish became infected naturally, and mortalities began occurring in

TABLE 1. Prevalence of bacterial kidney disease in newly stocked hatchery trout and wild trout collected from three stations on the French Creek–Brush Creek drainage system during 1977 and 1978 as determined by the fluorescent antibody technique of Bullock and Stuckey (1975).

	BKD positive/sample size							
	Mortalities				Live fish			
Station No.	Hatchery rainbow trout	Hatchery brown trout	Hatchery brook trout	Wild brook trout	Hatchery rainbow trout	Hatchery brown trout	Hatchery brook trout	Wild brook trout[a]
1	8/8	6/6	17/17	21/21	2/5	2/11	38/80	36/60
2	0/0	11/11	14/14	11/11	45/62	33/60	28/61	13/45
3	8/8	23/23	18/18	83/83	9/60	7/60	8/24	46/58
No. positive	16/16	40/40	49/49	115/115	56/137	42/131	74/165	95/163
% positive	100	100	100	100	41	32	45	58

[a]These live wild brook trout were collected in 1976 during an earlier study (Mitchum et al. 1979) and are included here for comparison.

FIG. 1. Typical signs of bacterial kidney disease (BKD) in affected hatchery brook trout (above; note excised right pelvic fin — arrow), hatchery brown trout (center), and hatchery rainbow trout (below) found dead in North French Creek. The frequency and extensiveness of the gross lesions which occurred in the kidney ranged in severity as follows: brook trout > brown trout > rainbow trout. Note also the circular, light-colored, BKD lesion in the liver of the brown trout.

9 mo or less. Natural infections of BKD in wild brook trout can occur in 2–6 mo or less (Mitchum et al. 1979), and losses from BKD can occur in 1–3 mo in Pacific salmon (Wood 1974).

Frantsi et al. (1975) presented evidence that salmonids located at a hatchery may become infected with BKD from a natural infection in wild fish present in the water supply. In a later study, Frantsi et al. (1977) reported that the stocking of infected hatchery salmonids may have had a "very serious effect" on natural salmonid populations in the watershed. However, Allison (1961), in examining 164 collected fish for clinical signs, could find no mortalities and no instances in which BKD was transmitted from infected stocked trout to fish present in several natural waters. But, mortalities could have gone undetected, and subclinical carrier infections may have been discovered by more sensitive detection methods (such as FAT) available today. The data of Allison (1961) on transmittance of BKD are in contrast to Mitchum et al. (1979), who found that BKD was transmitted from infected stocked hatchery trout to wild trout, and the data of this study where BKD was transmitted from infected wild trout to stocked hatchery salmonids.

Mortalities found were highest in the brook trout, lower in brown trout, and lowest in rainbow trout (Table 1). These mortality data on relative susceptibility of these trout species agree with those of Bullock et al. (1971). Also, our necropsies revealed that the frequency and extensiveness of the gross lesions ranged in severity as follows: brook trout > brown trout > rainbow trout. Kidneys in affected rainbow trout were often light-colored, slightly swollen, and contained moderate to large numbers of *R. salmoninarum*. In contrast, kidneys in affected brook trout and brown trout were typically light-colored, greatly swollen, and exhibited macroscopic grayish-white lesions containing great numbers of bacteria and necrotized tissue (Fig. 1). Exophthalmos (popeye) and abnormally dark-colored skin were evident in some fish of each species collected, but external skin lesions were not found in any dead or live trout.

Statistical analysis of disease incidence (Table 1) shows that the number of mortalities is not significantly different between hatchery brook trout and hatchery brown trout ($P > 0.05$, where P represents the significance level of a Chi-square test in a 2×2 contingency table), but data from the live fish show a significantly higher percentage of infected brook trout than brown trout ($P \simeq 0.025$). Numbers of dead fish found were significantly lower for stocked hatchery rainbow trout than for either brook trout or brown trout (Table 1; $P < 0.01$ for both tests), but the observed difference was not judged to be significant when the numbers of infected live hatchery rainbow trout were compared to either live hatchery brook trout or live hatchery brown trout (Table 1; $P > 0.05$). Statistical analysis of our data only supports the conclusion that the rainbow trout is the most refractory of the three species.

Detection of *R. salmoninarum* in BKD carriers or recently infected fish (1+ and 2+ severity infections, Mitchum et al. 1979), is often difficult even when using the FAT. During this study, we found that less severe infections were often detected at a higher rate when fecal rather than kidney samples were examined from a given fish. For example, the infection rate for the live sample of hatchery brook trout was determined to be 35% when feces were examined, but only 8% when kidney tissues were tested (Table 2). This trend also appeared in the samples of live stocked rainbow trout and brown trout. More severe infections (4+ and 3+) occurred in the dead trout samples, and the BKD organism was usually detected easily in both feces and kidney tissues (Table 2).

Because of limitations in the FAT for detecting BKD in subclinical infections, it is posible that some carriers (or newly infected fish) were undetected in the samples examined in this study. It is also possible that some carrier BKD infections would not be discovered in any given population, especially if only one tissue from each fish were examined. It is important to consider test limitations when surveying for any fish disease, but especially for BKD because of the organism's fastidious nature and slow growth on culture media. Still, FAT is the most sensitive diagnostic method presently in use, particularly where carrier-type infections are involved. Evelyn (1977) described a culture method which is reportedly also very sensitive in detecting BKD. This procedure, in conjuction with FAT, should be thoroughly field-tested. Perhaps, for greatest sensitivity, these methods should be used concurrently.

Some investigators have postulated that parasitic vectors, such as trematodes or copepods which penetrate skin and gill tissue, might be involved in the transmission of BKD (Snieszko and Griffin 1955; Wood and Yasutake 1956; Wolf and Dunbar 1959b; Allison 1961; Bullock et al. 1975). We

TABLE 2. Detection of *Renibacterium salmoninarum* in trout kidney tissues and fecal smears by the fluorescent antibody technique (Bullock and Stuckey 1975).

	BKD positive (% positive)							
	Live fish				Dead fish			
Material tested (sample size)	Hatchery rainbow trout (130)	Hatchery brown trout (68)	Hatchery brook trout (133)	Wild brook trout (25)	Hatchery rainbow trout (2)	Hatchery brown trout (26)	Hatchery brook trout (21)	Wild brook trout (74)
Kidney	9(7%)	4(6%)	10(8%)	2(8%)	—	—	—	—
Fecal	32(25%)	29(43%)	46(35%)	5(20%)	—	4(15%)	2(10%)	2(3%)
Kidney and fecal	14(11%)	2(3%)	13(10%)	4(16%)	2(100%)	22(85%)	19(91%)	72(98%)
Total	55(42%)	35(52%)	69(52%)	11(44%)	2(100%)	26(100%)	21(100%)	74(100%)

found no evidence in this study, or in an earlier study in the drainage system (Mitchum et al. 1979), to support this hypothesis. No parasites or viruses were found in the dead hatchery trout and wild trout collected during this study, but in addition to *R. salmoninarum*, 13 other bacterial species were isolated. Eight of these speices were also found in the dead wild trout necropsied during 1977 (Mitchum et al. 1979). The prevalence of these other bacteria was very low (most were isolated only once from only one fish); they are ubiquitous in nature; and they likely entered fish tissues after death as opportunistic secondary invaders. Only *Aeromonas hydrophila* and *Pseudomonas fluorescens* (also ubiquitous), isolated from only three and one dead trout, respectively, are known to cause disease in fish, and then only under high stress conditions. Because the BKD organism was found by FAT in all of the mortalities (Table 1) and because other known fish pathogens were either absent or found only occasionally in BKD infected fish, we believe that all of the deaths were due to BKD.

Acknowledgments — We gratefully acknowledge the assistance of the following personnel of the Wyoming Game and Fish Department: W. Donald Dexter, Jack Kanaly, Fred Eiserman, Joe White, Steve Facciani, and Chester C. Anderson for their administrative support; Mel Oberholtzer, Mike Yakimovich, Wayne Manore, Art Tanner, Ralph Garbutt, T. J. McCreery, and Tom D. Moore for their technical assistance; and W. G. Hepworth for editorial assistance. We also thank George Baxter and Lyman McDonald, University of Wyoming, for their technical assistance. We thank the USFWS National Fish Health Research Laboratory-Leetown, Kearneysville, W. VA, USA, for the standardized fish biologics used in the FAT. Critical reviews of the manuscript by G. L. Bullock and T. P. T. Evelyn are greatly appreciated. This work was supported in part by Federal Aid in Fish Restoration Wyoming Project FW-3-R.

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Evidence of *Salmo salar* × *Salmo trutta* Hybridization in a North American River

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Electrophoretic examination of 56 wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) from the Stewiacke River, Nova Scotia, revealed one individual believed to be a hybrid between these two species. The possibility of loss of the genetic integrity of each species is considered. A long history of sympatry between Atlantic salmon and brown trout in Europe may have prevented the formation of hybrid swarms as occurred in western North America following introduction of nonindigenous *Salmo*.

Key words: electrophoresis, introgression, enzymes, genetic interaction

BELAND, K. F., F. L. ROBERTS, AND R. L. SAUNDERS. 1981. Evidence of *Salmo salar* × *Salmo trutta* hybridization in a North American river. Can. J. Fish. Aquat. Sci. 38: 552–554.

Lors de l'examen électrophorétique de 56 saumons atlantiques et truites brunes sauvages de la rivière Stewiacke, en Nouvelle-Écosse, nous avons détecté un individu que nous croyons être un hybride entre ces deux espèces. Nous examinons la possibilité d'une perte d'intégrité génétique de chaque espèce. Il se peut qu'une longue histoire de sympatrie entre le saumon atlantique et la truite brune en Europe ait empêché la formation d'hybrides, comme cela c'est produit en Amérique du Nord occidentale à la suite de l'introduction de *Salmo* non indigènes.

Received August 5, 1980
Accepted February 3, 1981

Reçu le 5 août 1980
Accepté le 3 février 1981

THE occurrence of wild F_1 hybrids between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) has been confirmed by gel electrophoresis in Great Britain, where the two species occur sympatrically (Payne et al. 1972; Solomon and Child 1978). Other studies have confirmed the viability of artificially produced F_1 hybrids between these two species, as well as F_2 hybrids and backcrosses (Catt 1950; Alm 1955; Piggins 1965, 1966). Despite widespread introductions of brown trout into the salmon's native range (Catt 1950; MacCrimmon and Marshall 1968; MacCrimmon et al. 1970), reports from this continent of naturally occurring hybrids between Atlantic salmon and brown trout are lacking.

In western North America, the introduction of rainbow trout (*Salmo gairdneri*) into the native range of other trouts, such as the cutthroat (*Salmo clarki*) and golden (*Salmo aguabonita*) trouts, has resulted in hybrid swarms and widespread genic introgression between the indigenous and introduced species. Similar instances of hybridization and introgression between Atlantic salmon and brown trout have not been reported in North America. The morphological similarities between Atlantic salmon and brown trout would preclude the detection of hybrids by inexperienced observers. Atlantic salmon and brown trout also share an evolutionary history of coexistence in Europe, which would have favored reproductive isolation and selected against hybrids. In North America, only the Atlantic salmon is indigenous, whereas the brown trout was introduced relatively recently. The reproductive isolation between these two species may be fragile, which would allow more widespread introgression than observed in Europe.

This study attempted to determine what, if any, evidence of hybridization between these two species could be found in a North American river containing both Atlantic salmon and brown trout. One river that contains spawning populations of Atlantic salmon and brown trout is the Stewiacke, which is located in central Nova Scotia, and empties into the Bay of Fundy. Brown trout were first introduced into this river in 1952 (J. Ritter, Dep. of Fisheries and Oceans, Halifax, N.S., personal communication). In light of the potential impact of introduced salmonid species on indigenous ones, it would be desirable to assess the extent of genetic interaction between these two species in a river such as the Stewiacke.

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Printed in Canada (J6181)
Imprimé au Canada (J6181)

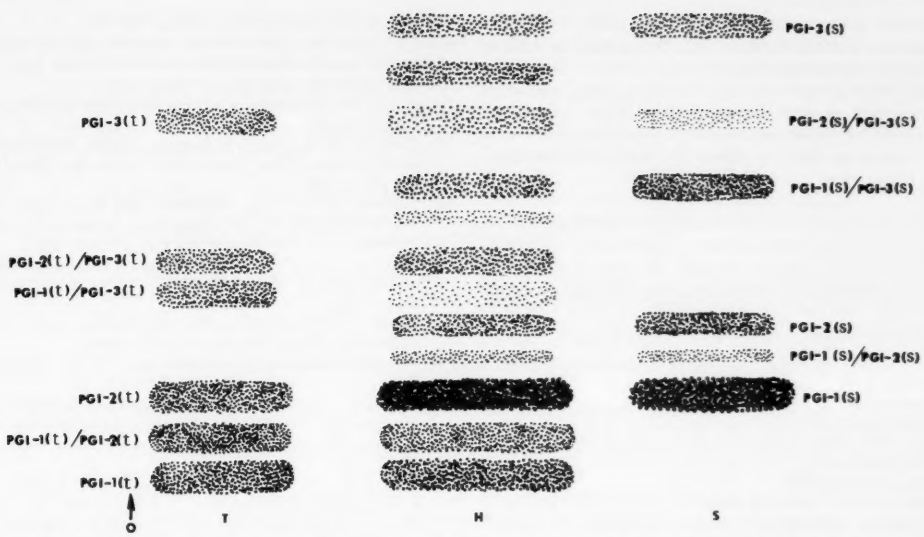

FIG. 1. Phosphoglucoseisomerase phenotypes in *Salmo trutta* (T), *Salmo salar* (S), and a hybrid between the two species (H). O indicates origin; t and s indicate trout and salmon bands.

Materials and methods — A total of 56 wild Atlantic salmon parr and brown trout were collected by electrofishing in late 1978 from Otter Brook, a tributary to the Stewiacke River, and frozen at −20°C for transport and storage. Muscle and liver extracts were prepared for electrophoresis by adding three drops of 0.20 mol/L Tris-HCl buffer, pH 8.0, containing two drops/mL 2-mercaptoethanol, to 0.5 g of tissue. The tissues were kept on ice and homogenized with a motor-driven grinder, and centrifuged at 2°C for 20 min at 20 000 × *g*. The supernatant was immediately used for electrophoresis.

Horizontal starch gel electrophoresis was adapted from the method of Selander et al. (1971). Gels prepared with 12% Electrostarch were poured into Plexiglas molds, and tissue extracts were inserted on 5-mm filter paper squares. The LiOH buffer system described by Selander et al. (1971) was used for all enzymes, and electrophoresis took 3.5 h at 350 V/55 mA. After electrophoresis, the gels were sliced in half and stained according to the methods of Allendorf et al. (1977), whose enzyme nomenclature was also used.

Results and discussion — Of the sample of 56 Stewiacke River *Salmo* examined, 42 were Atlantic salmon, and 13 were brown trout, based on comparisons with zymograms from salmon and trout of known origin. One specimen possessed isozyme patterns indicative of hybrid origin. Atlantic salmon and brown trout possess isozymes with different electrophoretic mobility at the four loci discussed in this study (Beland 1979). For the enzyme phosphoglucoseisomerase (PGI), Atlantic salmon and brown trout differ at two (PGI-2, PGI-3) of the three loci expressed in muscle. The two species also differ at a phosphoglucomutase (PGM) locus, and a liver esterase (EST-2) locus. The presumed hybrid showed both salmon and trout isozymes for the two PGI loci (Fig. 1), as well as for the EST locus. This same fish showed only the typical brown trout PGM isozyme.

These data suggest that this one specimen from the sample examined is of hybrid origin. The absence of the salmon PGM isozyme suggests that it may be the result of a backcross between a brown trout and an F_1 hybrid.

This evidence of hybridization between Atlantic salmon and brown trout in a North American river raises questions regarding the maintenance of genetic integrity of Atlantic salmon and brown trout in rivers where the two species coexist. If hybridization occurs frequently enough to result in significant genic introgression between the two species, the result could be the loss of a salmon or trout breeding population, and the fishery associated with it. This phenomenon has resulted in the loss of many populations of rare western North American *Salmo* due to widespread introductions of rainbow trout (Hubbs 1955; Behnke 1970, 1972; Schreck and Behnke 1971). The loss of an anadromous Atlantic salmon fishery would be considered serious, because of the high value placed upon sport fisheries for Atlantic salmon, and the diminishing number of Nova Scotia rivers which support Atlantic salmon. Whether a substitute fishery for salmon × trout hybrids would be as desirable to anglers would depend, in part, upon their size and abundance relative to the salmon and trout populations already present in the river.

The observation of only one specimen of probable hybrid origin in a sample of 56 wild Atlantic salmon and brown trout suggests that hybridization between the two species is not extensive in the Stewiacke River. This observation agrees with that of Payne et al. (1972) in the British Isles, where the incidence of hybrid fish was observed to be less than 1% in a sample of 4431 fish from 11 rivers. The apparent low incidence of hybridization between Atlantic salmon and

brown trout in the Stewiacke may indicate a similar degree of reproductive isolation between these two species as is found in European populations. Further study could provide a better estimate of the frequency of hybridization events, and allow an assessment of their impact on the Atlantic salmon and brown trout populations of this river. Such a study could make use of karyotype data, for salmon and trout differ considerably in karyotype (*S. salar* 2N = 54–56, *S. trutta* 2N = 80).

Acknowledgements — We thank Mr John Ritter and his staff from the Department of Fisheries and Oceans for providing the specimens used in this study. Dr Brian D. Glebe and Mr John K. Bailey gave helpful suggestions for preparing the manuscript. This research was supported through U.S. Fish and Wildlife Service contract No. 14-16-0009-013.

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Short-term Rearing of Pink Salmon (*Oncorhynchus gorbuscha*) Fry: Effect on Survival and Biomass of Returning Adults

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Survival of pink salmon (*Onchorynchus gorbuscha*) fry could theoretically be improved if they were reared to a larger size before being released into the estuary. Three lots of 1975-brood pink salmon fry, reared from eggs in a hatchery, were cultured in floating estuarine raceways for 30, 60, and 90 d before being released into the Little Port Walter estuary on Baranof Island, southeastern Alaska. An unfed control lot was released after emergence. Four groups of 15 000 fry each were differentially fin marked. Total marine survival for the four lots was computed from recoveries of marked adults in the Little Port Walter vicinity in 1977. Survival from release to return was lowest for the control lot (3.1%); increased for fry reared for 30 and 60 d (4.6 and 5.2%, respectively); and decreased for fry cultured for 90 d (4.3%). Mortalities in lots cultured for 60 and 90 d significantly reduced the numbers of fry released in these groups. Mortalities were associated with the marine diatoms *Chaetoceros* spp. Mean length and weight of returning adults declined with increased fry-

Printed in Canada (J6022)
Imprimé au Canada (J6022)

rearing time. Compared with the control lot, adults from fry cultured for 30 d had 39% more biomass; adults from fry cultured for 60 d had the same biomass; and adults from fry cultured for 90 d had 45% less biomass. Culturing fry for 30 d in the raceways significantly increased the number and biomass of returning adults.

Key words: short-term rearing, *Oncorhynchus gorbuscha*, floating estuarine raceways, marine survival, biomass

MARTIN, R. M., W. R. HEARD, AND A. C. WERTHEIMER. 1981. Short-term rearing of pink salmon (*Oncorhynchus gorbuscha*) fry: effect on survival and biomass of returning adults. Can. J. Fish. Aquat. Sci. 38: 554–558.

En théorie, la survie d'alevins de saumon rose serait améliorée si l'on pouvait les élever à une plus grande taille avant de les libérer dans l'estuaire. Nous avons maintenu pendant 30, 60 et 90 jours, dans des passes à poissons estuariennes flottantes, trois lots d'alevins de saumons rose (*Oncorhynchus gorbuscha*) de la portée de 1975, élevés dans une écloserie à partir de l'œuf, pour les libérer ensuite dans l'estuaire de Little Port Walter, dans l'île Baranof,, au sud-est de l'Alaska. Nous avons libéré après émergence un lot témoin non nourri. Quatre groupes de 15 000 alevins chacun furent marqués de façon différente aux nageoires. Les recaptures d'adultes marqués dans le voisinage de Little Port Walter en 1977 ont servi à calculer la survie totale en mer des quatre lots. La survie depuis la mise en liberté jusqu'au retour était la plus faible dans le lot témoin (3,1%); augmenta avec les alevins maintenus durant 30 et 60 jours (4,6% et 5,2% respectivement); et diminua avec des alevins maintenus durant 90 jours (4,3%). La mortalité dans les lots élevés durant 60 et 90 jours eut pour effet de réduire considérablement le nombre d'alevins de ces groupes remis en liberté. Les diatomées marines *Chætoceros* spp. étaient responsables de ces mortalités. La longueur et le poids moyens des adultes qui revinrent diminuèrent avec l'augmentation de la période d'élevage des alevins. Comparativement au lot témoin, les adultes provenant d'alevins élevés durant 30 jours avaient une biomasse de 39% supérieure, les adultes provenant d'alevins élevés durant 60 jours avaient la même biomasse; et les adultes provenant d'alevins élevés durant 90 jours avaient une biomasse de 45% inférieure. Le maintien des alevins durant 30 jours dans les passes cause une augmentation significative du nombre et de la biomasse d'adultes qui reviennent.

Received March 31, 1980
Accepted February 2, 1981

Reçu le 31 mars 1980
Accepté le 2 février 1981

BECAUSE pink salmon begin their marine life as recently emerged fry, they are subject to greater marine mortality than species not migrating from freshwater until they are older and larger. Smaller, younger pink salmon in nearshore coastal areas have a higher mortality than larger, older pink salmon in ocean areas (Parker 1965). An estimated 77% of the 55.7 million pink salmon fry from the 1961-brood year in the Burke Channel, Bella Coola, British Columbia, died during their first 40 d of marine life (Parker 1965).

Theoretically, survival of pink salmon could be improved if fry are raised to a larger size and are released without disrupting their time and pattern of ocean migration. To explore this possibility, we released pink salmon fry that were fed in raceways for 30, 60, and 90 d after emergence. This experimental design represents only one subset of a large number of potential rearing strategies for pink salmon fry. In this paper, we describe the effects of these different feeding periods on survival, mean length, mean weight, and biomass of returning adults.

Methods — The study was conducted at the National Marine Fisheries Service experimental aquacultural facility at Little Port Walter, Baranof Island, Alaska (Fig. 1). Eggs were collected from adult pink salmon of the 1975 brood when the adults migrated through a weir located on Sashin Creek at the head of tidewater in Little Port Walter Bay. A total of 833 000 eyed pink salmon eggs were seeded in eight incubators that had gravel substrate and upwelling water. The incubators are similar to those described by Bailey and Taylor (1974). Subsequently, 749 700 fry were produced; some fry were used for other purposes.

As fry emerged from the incubators, four lots of 15 000 fry each were differentially marked by excising combinations of ventral and adipose fins. From 12 to 34% of all the fry in the incubators emerged between April 13 and 20. All four lots of fry were marked simultaneously within this period. The excised fins were left ventral fin (LV), control lot; right ventral fin (RV), 30-d release; adipose and right ventral fins (Ad-RV), 60-d release; and adipose and left ventral fins (Ad-LV), 90-d release. Each day, the same number of fry were marked from each lot and held for 24 h so that initial marking and handling losses could be replaced. After the 24-h holding period, the control lot was released unfed into the estuary, and the other three lots were released into separate raceways. This process was repeated daily until 15 000 live, marked fish were present in each lot.

The three retained lots were reared in floating, vertical raceways (Heard and Martin 1979) for 30, 60, and 90 d

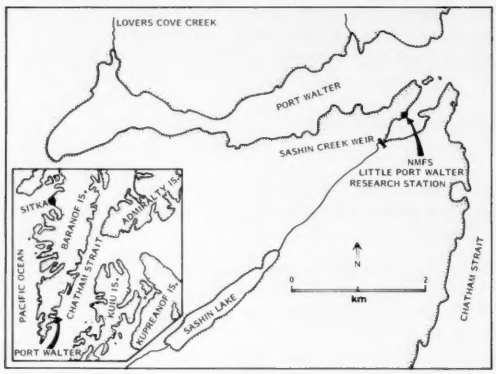

FIG. 1. Location of National Marine Fisheries Service Little Port Walter Biological Field Station, Port Walter drainage, Baranof Island, Alaska.

beyond the midpoint of marking, April 18. During culture, the fry were fed Oregon Moist Pellets[1] to satiation 10–16 times per day. Water flowing through the raceways was maintained at 18–20‰ salinity by a venturi device (Heard and Salter 1978).

Just before release, fry from the 30-, 60-, and 90-d lots were individually counted (Table 1). The adipose fins of 1000 fry from the 60-d lot and 1000 fry from the 90-d lot were examined to determine the possibility of misidentifying double fin marks as single fin marks. The 60-d sample contained no poor adipose-fin marks, whereas the 90-d sample had three poor marks — a rate of 0.3%, which we considered low enough to be ignored. The number of unmarked incubator fry released into the estuary was estimated gravimetrically; the number of wild fry entering the estuary from Sashin Creek was estimated by hydraulic sampling (McNeil 1964) before the fry emigrated.

Adult pink salmon of the 1975 brood were captured and examined in 1977 when they passed through the weir on Sashin Creek. Length, weight, and sex data were obtained from samples of marked adults from each of the four lots and from samples of unmarked adults. All pink salmon counted through the weir were individually examined for fin marks and for evidence of regeneration of the ventral fins (broken or interrupted fin rays).

Ventral fins of pink salmon may regenerate, but adipose fins do not. Sockeye salmon (*O. nerka*) fingerlings held in seawater for 2 yr after finclipping showed no regeneration of the adipose fin (Weber and Wahle 1969). In a similar study, also with sockeye salmon, Worlund et al. (1969) found no regeneration of the adipose fin. Regeneration of the ventral fin does occur, but the regenerated fin is usually less than 25% of its original size (Worlund et al. 1969). Even when regeneration of the ventral fin is greater than 25%, the mark is readily identifiable because the fin rays are deformed (Worlund et al. 1969).

[1]Reference to trade names does not imply endorsement by National Marine Fisheries Service, NOAA.

Some of the pink salmon were caught in a purse–seine fishery for coho salmon (*O. kisutch*) in the Port Walter area. Others spawned in the intertidal portion of Sashin Creek, downstream from the weir. We examined 21% of the pink salmon caught in the purse–seine fishery for marks. Fish that spawned in the intertidal portion of Sashin Creek were not examined for marks but were apportioned into the four marked lots according to the ratios determined for marked fish passing through the weir.

We calculated chi-square values for simultaneous comparisons (Goodman 1964) to test for significant differences among the marked groups of fish. In testing size difference among the marked groups, we used Tukey's test for honest least significant difference for multiple comparisons (Steel and Torrie 1960) to identify homogenous populations, i.e. groups that were not significantly different at $P = 0.05$. Instantaneous rates of total mortality (Ricker 1975) were calculated for marked fry from the control lot and for unmarked fry from Sashin Creek and hatchery incubators to determine whether marking affected marine survival. The instantaneous rate of total mortality, Z, can be determined from the survival rate, s, by the formula $Z = -\ln(s)$ (Ricker 1975).

Results — In 1977, 28 497 pink salmon returned to the weir on Sashin Creek; an estimated 1500 pink salmon spawned in the intertidal portion of the creek; and 5507 pink salmon were caught during the purse–seine fishery. We examined 1175 fish caught in the fishery for fin marks, and 2.8% had missing fins. Based on an extrapolation of the marked rate in the seine catch and the marked rate of adults at the weir (0.028/0.062), we assigned 45.2% (2487 fish) of the seine catch to Sashin Creek. The total return to Sashin Creek, including intertidal spawners, seine catch, and weir count was 32 484, of which 87.7% was sampled at the weir for marks. The time of entry of marked and unmarked fish into the stream appeared to be similar.

Survival calculated from number of fry released that returned as adults was lowest for the control lot, 3.1%; increased to 4.6 and 5.2% for the 30-d and 60-d lots, respectively; then decreased to 4.3% for the 90-d lot (Table 1). There was a significant difference in marine survival between the control lot and each of the experimental lots ($P < 0.005$). Survivals of the 60-d and the 90-d lots were significantly different ($P < 0.10$). The other two comparisons, 30-d versus 60-d and 30-d versus 90-d, did not differ significantly.

Survival of unmarked fry from Sashin Creek and hatchery incubators and survival of marked fry from the control lot were surprisingly similar, 3.4% for unmarked fry and 3.1% for marked fry. The instantaneous-mortality rate (Ricker 1975) for our marked control lot was 3.48, and the rate for unmarked fish was 3.39, a handicap ratio of 1.03.

During the first 45 d of culture, few fish died; but after that, mortality increased rapidly and then remained nearly constant at the new higher rate. The Alaska Department of Fish and Game Pathology Laboratory determined that the marine diatoms *Chaetoceros* spp. caused deaths by clogging gill filaments. *Chaetoceros convolutus* has killed other marine-cultured juvenile salmon (Kennedy et al. 1977). Between marking and release, 0.9% of the fry from the 30-d lot died; however, 39% of the 60-d lot and 49% of the 90-d lot died between marking and release. Thus, there was a difference in

TABLE 1. Summary of the survival of 1975-brood pink salmon (*Oncorhynchus gorbuscha*) fry at Little Port Walter, Alaska. Marked fry are from the three cultured lots and one control lot. The unmarked fry were from other incubators at Little Port Walter and from natural spawning. Fish were marked by excising either the left ventral fin (LV), the right ventral fin (RV), the adipose and right ventral fins (Ad-RV), or the adipose and left ventral fins (Ad-LV). Numbers in parentheses are standard deviations.

Fin mark	Days reared	Number marked	Number released	Mean size at release: Weight (g)	Mean size at release: Forklength (mm)	Number of adults at Sashin Creek weir[a]	Estimated[a] number of adults returning to Port Walter	Survival: of number released (%)	Survival: of number marked (%)
LV	0	15 000	15 000	0.23	32.0 (±0.88)	407	464	3.1	3.1
RV	30	15 000	14 862[b]	0.27	34.7 (±2.39)	594	677	4.6	4.5
Ad-RV	60	15 000	10 034[b]	0.55	39.9 (±6.82)	458	522	5.2	3.5
Ad-LV	90	15 000	7 608[b]	1.95	58.6 (±9.64)	289	330	4.3	2.2
Unmarked	0	0	904 205[c]	0.23[d]	32.0[d]	26 749	30 501	3.4	—

[a]Numbers of adults recovered from the weir were expanded by 0.877 to include estimates of intertidal spawning and adults caught in a special seine fishery.

[b]Difference between number marked and number released is primarily due to mortalities from *Chaetoceros* spp. during rearing.

[c]Based on 681 764 unmarked fry from the incubators and 222 441 wild fry.

[d]Mean size of fry at emergence from the incubators.

TABLE 2. Comparison of lengths and weights of marked and unmarked pink salmon adults recovered at Sashin Creek weir, 1977.

Lot	Sample size	Mean length[a] (cm)	Mean weight (kg)
		Male	
Unmarked	109	52.5	2.44
Control	109	51.8	2.29
30-d	109	50.0	2.04
60-d	109	49.8	1.98
90-d	109	47.4	1.65
		Female	
Unmarked	85	51.8	2.05
Control	85	51.4	2.04
30-d	86	51.1	2.06
60-d	85	50.0	1.87
90-d	87	48.6	1.69

[a]Length was measured from midorbit of the eye to fork of the caudal fin.

TABLE 3. Biomass of marked adult pink salmon returning to Port Walter, 1977.

Lot	No.	Mean weight (kg)	Biomass produced: Total (kg)	Biomass produced: Per fry (kg)
Control	464	2.17	1007	0.067
30-d	677	2.05	1388	0.093
60-d	522	1.93	1007	0.067
90-d	330	1.67	551	0.037

some groups between survival calculated from the number of fry marked (15 000) and survival calculated from the number of fry released (Table 1).

Mean length of both males and females decreased with increased rearing time. Mean weight also decreased with increased rearing time, except females from the 30-d lot were slightly heavier than females from the control lot. Unmarked fish were longer and heavier than marked fish of the control lot for both males and females (Table 2). Using Tukey's test, we identified the following groups as homogenous (not significantly different at $P = 0.05$) in both length and weight: for males (1) unmarked fish and control lot, (2) 30-d and 60-d lots, and (3) 90-d lot; for females (1) unmarked fish, control lot, and 30-d lot; (2) 60-d lot; and (3) 90-d lot.

We estimated the biomass of adult pink salmon produced from each lot by multiplying the mean weight of fish from each lot caught at the weir by the estimated number of fish from each lot returning to Port Walter (Table 3). Compared to the control lot, the 30-d lot produced 39% more biomass; the 60-d lot produced the same biomass; and the 90-d lot produced 45% less biomass.

Discussion — Optimum time for rearing fry in the hatchery probably varies slightly from year to year and depends on environmental conditions such as estuarine temperature and plankton blooms. Rearing fry in the hatchery for 30 d, the optimum rearing time in this study, increased the number and biomass of returning adult fish. The slight decrease in mean weight of adults from the 30-d lot compared to the control lot was more than offset by the increased marine survival of the 30-d lot. Although marine survival of the 60- and 90-d lots was greater than marine survival of the control lot, the difference between survival calculated from the number of fry marked (15 000) and survival calculated from number of fry released clearly shows that possible survival advantages of short-term reared pink salmon may be negated by mortality during rearing (Table 1).

The control and 30-d lots (marked RV or LV) were probably more vulnerable to predation when released because they were held less time after marking and were smaller than the 60- and 90-d lots. Newly marked pink salmon fry are more susceptible to predation than unmarked fry (Parker et al. 1963); however, this difference in susceptibility may be reduced by holding marked fish until effects of fatigue are over and injuries are healed (Parker et al. 1963). Differential susceptibility to predation because of fin removal should decrease, but probably not completely disappear, with increased rearing time. Small pink salmon juveniles are

preyed upon more than large juveniles (Parker 1971); however, this effect may have been offset by the multiple fin marks of the 60- and 90-d lots (marked Ad-RV and Ad-LV). Mears and Hatch (1976) show that removal of more than one fin further reduces overwinter survival of fingerling brook trout, *Salvelinus fontinalis*.

Fin marking probably adversely affected survival of fry in the control lot; however, release of the fry may have coincided with a particularly advantageous period in the estuary. Ricker (1976) reports greatly reduced survival for marked pink salmon. In his studies, handicap ratios for the instantaneous-mortality rates of marked to unmarked fry ranged from 1.119 to 1.575. In our study, the 95% confidence interval for marine survival of unmarked fry was wide. If we used the upper limit of the confidence interval for survival, 3.9%, the instantaneous-mortality rate was 3.26, and the handicap ratio was 1.07 — a handicap ratio still far below the values given by Ricker. The difference between our handicap ratios and Ricker's may be indicative of the importance of timing of emergence of pink salmon fry from spawning gravel and the differential survival rates of fry from different segments of the fry-emigration period.

From 1940 to 1979, marine survival of pink salmon fry from Sashin Creek has varied 115-fold, from 0.2 to 23.1% (Ellis 1969; A. C. Vallion, A. C. Wertheimer, W. R. Heard, and R. M. Martin, Northwest and Alaska Fisheries Center Auke Bay Laboratory, P.O. Box 155, Auke Bay, AK, USA, 1980, unpublished data). During the first 40 d of marine life, survivals of pink salmon fry in the Bella Coola estuary were 23, 45, and 41% for 1961-, 1962-, and 1963-brood years, respectively (Parker 1968). Such fluctuations in early marine survival may be responsible for the wide variations in overall marine survival. As demonstrated in this study, culturing the fish during an unstable period of early marine life might reduce year-to-year variability in overall marine survival.

Acknowledgments — We thank Jeffrey Fujioka for assistance in the statistical calculations; Tia Landon for compilations of data; and Peggy Wertheimer, Roger Vallion, Randy Riddell, Dick Crone, Steve Schmitt, Roger Grischkowsky, and Al Didier for their assistance in various aspects of the diverse fieldwork associated with this study.

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Recreational Fisheries Analysis: Management Modes and Benefit Implications[1]

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COPES, P., AND J. L. KNETSCH. 1981. Recreational fisheries analysis: management modes and benefit implications. Can. J. Fish. Aquat. Sci. 38: 559–570.

The analysis of recreational fisheries management is a relatively neglected area of research. In this paper we have attempted to advance that analysis by adapting certain theoretical considerations that have been used in (commercial) fisheries economics and in recreational economics. Specifically, we have considered the implications of the different modes of management that would be expected to prevail under the different management regimes of a public authority, a private owner, and a private club. We have also commented on the problems of integrating management in fisheries utilized for both commercial and recreational purposes and on measuring recreational fisheries benefits.

Key words: recreational fishing, management, limitation of entry, common property resource, benefit cost measurement, rationalization, property rights

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L'analyse de la gestion des pêches récréatives est un domaine de recherche relativement négligé. Dans l'article qui suit, nous voulons faire progresser cette analyse en adaptant certaines considérations théoriques qui ont été utilisées dans l'économie des pêches (commerciales) et celle de la pêche récréative. Plus précisément, nous examinons les implications de différents modes de gestion qu'on s'attendrait de rencontrer sous différents régimes de gestion, autorité publique, propriétaire particulier ou club privé. Nous offrons également des commentaires sur les problèmes d'intégration de la gestion dans des pêches à la fois commerciales et sportives, et sur la mesure des avantages retirés des pêches récréatives.

Received October 23, 1979
Accepted January 30, 1981

Reçu le 23 octobre 1979
Accepté le 30 janvier 1981

BOTH recreational and commercial fisheries have been the subject of theoretical analysis in the literature of economics. But there has been a notable dichotomy in the analytical approaches pursued, which has tended to separate the bodies of literature concerned with these two forms of fishing activity. In studying the commercial fisheries, economists generally have proceeded in their analysis from a consideration of fundamental bioeconomic relationships between sustainable yields and levels of fishing effort (Gordon 1954; Scott 1955; Turvey 1964; Smith 1969; Copes 1972; Clark and Munro 1975). From a different perspective, economists have analyzed sport fishing as a form of outdoor recreation. In doing so, they have tended to concentrate on the measurement of the revealed demand of consumers for opportunities to fish as a recreational pursuit (Crutchfield 1962; Brown et al. 1964; Scott 1965; Clawson and Knetsch 1966; Sewell and Rostron 1970; Gordon et al. 1973; McConnell and Norton 1976; Dwyer and Bowes 1978; McConnell 1980; Cauvin 1980).

In both areas of analysis attempts have been made to establish criteria for optimum utilization of the resource, in terms of the magnitude of net social benefits generated. However, efforts to integrate the respective analyses of commercial and sport fishing have been few in number. One early example of integrative analysis is that of Mathews and Wendler (1968), which concentrates on valuation of the catch taken by the two sectors. More recently, McConnell and Sutinen (1979) have elaborated a bioeconomic analysis of recreational fishing, including interaction with the commercial sector. Other contributions in this area have been made by Rothschild et al. (1977) and by Bishop and Samples (1980).

The purpose of this paper is to extend the theoretical anal-

[1]This is a revised and updated version of a paper initially presented at the Canadian Sports Fisheries Conference held inToronto, July 14–16, 1976. The original paper, entitled "Management Options and Management Intergration in Recreational and Commercial Fisheries," was commissioned by the Recreational Fisheries Branch of Environment Canada. The authors remain solely responsible for the contents of the paper, which do not necessarily reflect a position of the Canadian government or any of its agencies.

Printed in Canada (J5829)
Imprimé au Canada (J5829)

ysis of recreational fisheries management in a manner allowing for a link with commercial fisheries analysis. A common framework of management modes for the two sectors will be developed, related to common criteria of optimization. This framework will be compatible with, and linked to, both the bioeconomic analysis applied to commercial fisheries and the evaluative analysis underlying recreational economics as applied to sport fishing. The development of a common analytical base for commercial and sport fisheries is essential if rational policy decisions are to be made in the management of fish stocks that are jointly exploited by commercial and sports fishermen. While this paper will refer to common considerations in recreational and commercial fisheries management, its focus is on recreational fisheries, so that it will not extend to a comprehensive analysis of integrated management of the two fisheries sectors.

The management modes specified in this paper are concerned primarily with alternative institutional arrangements that affect the volume of net benefits generated in a fishery, as well as the distribution of these benefits among different interest groups. The beneficiary groups under consideration include various combinations of fishermen, consumers, private owners of the fishery resource, and the general public. The analysis will seek to establish in the case of each management mode, what benefits accrue to each group under what criteria of optimization. The paper will not be concerned with technical management questions of a biological or administrative character. For the sake of expository simplicity it will use the comparative static analysis common to much of the fisheries economics literature, abstracting from dynamic considerations of discount rates and price changes.

In an address before the Expert Consultation on the Economic Evaluation of Sport and Commercial Fisheries in Europe, held in Gothenburg in September 1975, Tuomi stressed the need for an analytical framework for social management decisions in recreational fishing similar to one that had been developed in respect of commercial fishing (Tuomi 1975). His reference was to an article by one of us analyzing exploitation equilibria in commercial fisheries under alternative forms of management and market organization (Copes 1972). This paper extends this analysis into the area of recreational fishing.

Management Modes for Commercial Fisheries

Following is a brief review, in intuitive terms, of the insights and conclusions emerging from the Copes (1972) article in respect of commercial fisheries exploitation. The various management modes that occur in commercial fisheries may be compared in terms of their effect on the generation of three categories of net social benefits. These are:

1) A consumers' surplus, measuring the difference between the magnitude of utility enjoyed by consumers from a given amount of a commodity (fish, in this case) and the market cost to them of acquiring it. It is, essentially, what the fish is worth to consumers (i.e. what they are *willing* to pay) − over and above what they *have* to pay. The consumers' surplus will be greater the lower the price paid and the greater the amount of the commodity acquired by consumers.
2) A producers' surplus, measuring the difference between the revenue received by fishermen for their catch and their costs of operation, including the opportunity cost of their labor; i.e. the amount they would receive for their labor in the best alternative employment. It is, essentially, what it is worth to a fisherman to be a fisherman rather than something else. The amount of producers' surplus generated will be greater, the higher the revenue received by each fisherman in relation to his costs and the larger the number of fishermen receiving such net returns. Larger producers' surpluses are likely to be earned by fishermen who are particularly skilled and thus have bigger catches and revenues, and by fishermen who have particularly low costs.
   Strictly speaking, "psychic" revenue must be included in the calculation, as well as market revenue. If a fisherman enjoys his occupation better than any other work, the value of this enjoyment should be added to the money revenue received for his catch. The producers' surplus is often referred to as a form of economic "rent," as it represents payment received by producers for the use of inputs they own or control over and above the amount necessary to prevent these inputs from being used for another purpose.
3) A resource rent, measuring the surplus revenue that could be appropriated by the owner of a fishery resource who is exploiting the resource to his best pecuniary advantage. Most fisheries have been common property resources to which fishermen have open access. With no one managing the resource for a profit, usually no resource rent is generated. One may imagine, however, a company or person being given the sole right to exploit a particular fish stock; then contracting with fishermen to bring in the catch; and then selling the catch to consumers. The resource owner's own net returns constitute the rent derived from the resource. This rent relates to the richness of the resource, which is a free gift of nature. It will be greater the more attractive the fish species is to consumers, so that they will pay more, and the easier the fish is to catch, so that costs of fishing may be kept down.

There are five distinct modes of access management, relating to different interest groups controlling access to the fishery resource to maximize their respective net benefits from fisheries exploitation (see Table 1). The first case, that of free access to the fishery, is a limiting case. This is the case, one might say, of zero access management, in which no interest group exercises control over the extent of fishing, so that no concerted effort can be made to maximize benefits.Until recently free access was the most common proximate condition in fisheries around the world. The literature on fisheries economics that has developed over the past 25 years has focused particularly on this condition of free access to a common property resource. It is now widely recognized that this condition commonly leads to the dissipation of all of the resource rent, i.e. all of the potential net benefits that are

TABLE 1. Characteristics of equilibrium levels of effort in a commercial fishery under different modes of access management (adapted from Copes 1972).

Form of access management	Categories of social benefits maximized	Incidental amounts of social benefit	Social benefits dissipated	Relation to socially optimum catch	Relation of consumers' price to social optimum	Relation to socially optimum level of effort
(A) Free access and free market	—	Consumers' surplus and producers' surplus	Resource rent	Indeterminate	Indeterminate	Above optimum
(B) Public management for maximum net social benefits	Combined total of consumers' surplus, resource rent, and producers' surplus	—	—	Optimal	Optimal	Optimal
(C) Consumers' monopsony	Combined total of consumers' surplus and resource rent	Producers' surplus	—	Below optimum	Above optimum	Below optimum
(D) Producers' monopoly	Combined total of producers' surplus and resource rent	Consumers' surplus	—	Below optimum	Above optimum	Below optimum
(E) Resource owners' monopoly	Resource rent	Consumers' surplus and producers' surplus	—	Below optimum	Above optimum	Below optimum

attributable to the resource itself.

The reason for this is simple. So long as access to the fishery is free and fish can be caught at a cost (including the "opportunity cost" of the fisherman's labor) below market price, the excess of revenue over costs will constitute a net benefit (i.e. the "resource rent") that will attract additional fishermen. However, the effort of these additional fishermen will have the effect of reducing stock density and thus the catch per unit of effort available to fishermen already in the industry. This will raise costs per unit of catch. The influx of additional fishermen will continue until costs per unit of catch have risen to a level equal to the market price per unit of catch, and there is no longer a net benefit to attract further fishermen. The number of fishermen is then stabilized. At this point all of the resource rent potentially available has been dissipated. It has been squeezed out by escalating costs that have risen to a level equal to the market price for fish.

It should be noted that it is the peculiar common property and open access nature of the fishery that leads to the dissipation of net benefits in the form of resource rent. A farmer doesn't let outsiders invade his land and harvest his crops. The farmer protects and retains the resource rent that his operations allow. But a fishermen cannot stop others from joining the fishery and catching "his" (?) fish. In the open access fishery there is a hidden social cost. When an additional fisherman decides to join the fishery, he counts only his own fishing costs against the revenue of his catch. But he imposes a multiplicity of costs on fellow fishermen whose catches are reduced by his effort. In social cost/benefit terms, the actual fishing costs of the additional fisherman plus the costs he imposes on the fishermen already in the industry will often exceed the value of the additional catch. Thus an open access fishery, taken as a whole, will face shrinking net benefits as additional operators join the fishery.

In the worst case, the effort of additional fishermen will not only reduce economic returns, but will also reduce (in the long run) the physical size of the catch because of the adverse effect on regeneration of the fish stock. This is the case of biological overfishing.

On the other hand, it should be noted that even where a stock is seriously overexploited, some net benefits may still accrue to society. Incidental amounts of consumers' surplus will be enjoyed by the more appreciative consumers, and incidental amounts of producers' surplus will be gained by ("intramarginal") fishermen with particularly high skills or particularly low costs.

Free access to a common property resource is in effect a form of economic anarchy, where no purposeful determination is made of the appropriate rate of utilization of the resource. In contrast to this state is a mode of public access management that attempts, in the interests of the general welfare of society, to maximize the sum total of net benefits to society, viz. the combined total of consumers' surplus, producers' surplus, and resource rent that may be derived from utilization of a fishery resource (case B in Table 1).[2] What is required in such a form of management is a limitation of effort to a level that will produce a catch with which maximum net benefits may be achieved. These net benefits, in essence, are the difference between the total utility enjoyed by consumers of fish and the real costs of

[2]We are abstracting here from welfare questions concerned with the distribution of these net benefits among different individuals in society. The underlying assumption is that if the distribution is not satisfactory from an equity standpoint, the state may correct by taxing the benefits of those who have too much and making disbursements to those who have too little.

production. Effort must be restricted below the level that would prevail under free access to eliminate the unnecessary fishing costs related to the employment of excessive numbers of fishing units that are attracted under free access.

Public managers require three sets of data to determine the optimum level of fishing effort: they need to have estimates of the demand function for fish; the pattern of private costs for the fishing fleet; and bioeconomic information to estimate the relationship between fishing effort and yield. Effort may be limited to the "right" level by licensing only the required number of fishing units. Alternatively, fishing operators may be charged fees at such a level that a sufficient number of fishermen is induced to leave the industry, so as to bring effort back to the appropriate level.

It has been suggested that one way of rationalizing exploitation of a fishery resource is to give sole ownership of the resource to a single individual or company (e.g. Scott 1955). The owner will have an interest in securing the greatest net benefit (i.e. the rent) from the resource that he possesses and will limit the effort applied to the resource to achieve it (see case E in Table 1).

The resource owner, however, is not likely to have any interest in the consumers' surplus going to the customers that buy his fish or the producers' surplus of the fishermen he employs or with whom he contracts. He will tend to set a relatively high price for fish to maximize his rent. This will limit net benefits (consumers' surplus) to his customers. But at a high price the amount of catch that can be sold will be reduced, calling for a curtailment of fishing effort, which in turn will involve a lower level of employment of fishermen. In pursuing his interest, the resource owner will also tend to keep down the price offered for fish landed by fishermen, further curtailing employment of marginal fishermen. On both counts the amount of producers' surplus that can be generated will be limited. In concentrating only on the maximization of resource rent, management by a resource owner will not achieve the maximum net social benefit attainable under a public management regime that would maximize the aggregate of consumers' surplus, producers' surplus, and resource rent.

In particular instances resource owners will be interested in the magnitude of either the consumers' or producers' surpluses that may be generated. If a consumers' cooperative is given ownership rights to a fish stock (or sole buying power), with the output to be used by its own members, it will be able to maximize total net benefits to its members, consisting of the combined total of its members consumers' surplus and the rent that the resource they own will yield to them (case C in Table 1). However, the cooperative will have no interest in enhancing the producers' surplus that will go to the fishermen they employ or with whom they contract. As a result, they are likely to reduce employment, and thereby the catch, to a level below the social optimum.

Conversely, if a producers' cooperative has sole access to a fish resource, it will presumably want to maximize the combination of resource rent and producers' surplus for its members (case D in Table 1). The producers' cooperative will not be concerned with consumers' surplus and will be inclined to raise prices against consumers to the level that will most benefit its members. Higher prices to consumers will reduce sales, and thereby also catch and effort, to levels below the social optimum.

The Nature of Recreational Fisheries

There are distinct difficulties in subjecting recreational fisheries to the kind of economic analysis of commercial fisheries used above. These difficulties stem from the unique character of the product and the production process in recreational fisheries, where the output is not to be measured in quantities of fish caught, but rather in the less tangible (if no less real) enjoyment of fishing. The quantity of fish caught is an incidental, though not unimportant, ingredient of the values created. While catching success usually enhances recreational enjoyment, it is possible to catch too much fish so that the "sport" is lost from sport fishing. The natural setting is a significant factor in the creation of recreational fishing values, while it may be ignored in commercial fisheries. Site crowding is quite an important consideration in sport fishing which less often needs to be considered in commercial operations. A number of attitudinal surveys carried out in Canada has demonstrated strongly that lack of crowding is generally a more important consideration in recreational fishing than number or size of fish caught (Bryan 1974; Radford and Wiebe 1975; Cox 1976).

To integrate commercial and recreational fisheries theory, it is necessary to relate both to common denominators. One of these, obviously, must be the amount of fish taken, for it is in the joint utilization of a stock of fish that interaction is most significant. This means that the nature of the complex relationship between the value of sport fishing enjoyment and the amount of fish taken must be determined. Of course, in sport fisheries, as in commercial fisheries, the size of the catch is related to the level of fishing effort. Participation in sport fisheries, measured for instance in person-days of fishing, may be considered an index of effort. Subject to an important qualification to be taken up in a later section, it will be held that the economic value of a product, such as fish, or a service, such as sports fishing opportunity, is what people are willing to give up to obtain it. This is the familiar concept of an amount put in monetary terms, which users would be "willing to pay" for the product or service provided. An alternative concept, the amount required in compensation to forego a good or service, will be considered at a later point.

A willingness to pay figure is an expression of real economic value, whether the products or services are directly priced to the consumer, as is the case with commercial fishery products, or whether they are provided free, as is often the case with sports fishing opportunities. Much of the latter, as with publicly provided recreation generally, is not priced and paid for by the direct beneficiaries of the service. But this nonmarket nature of the service, where money is not actually exchanged, does not make the economic value less real. It does, however, pose severe problems for its measurement.

To examine the value question further, reference may be made to a demand curve for the services of an isolated recreational fishery, i.e. one that is not interacting with a commercial fishery, as in Fig. 1. Here we may take the line AB to represent the demand curve for fishing opportunities in the area concerned. For this particular fishery, if there were no price charged for the fishing opportunity, nor any other

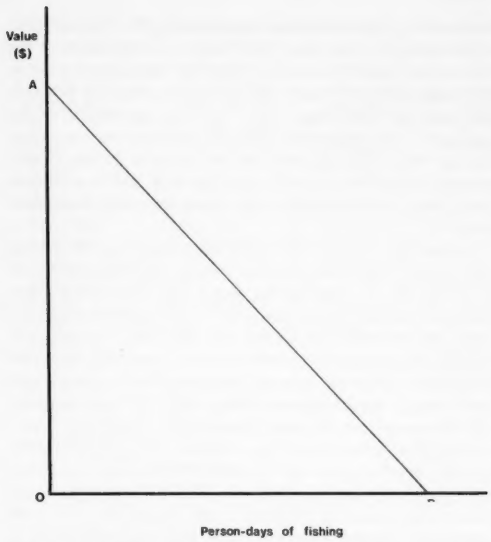

FIG. 1. Each point on this demand curve measures the answer to the question: "How much would you be prepared to pay to be allowed to participate for 1 day in this fishery, under the circumstance that all potential participants with higher evaluations are already participating, while no potential participants with lower evaluations are participating."

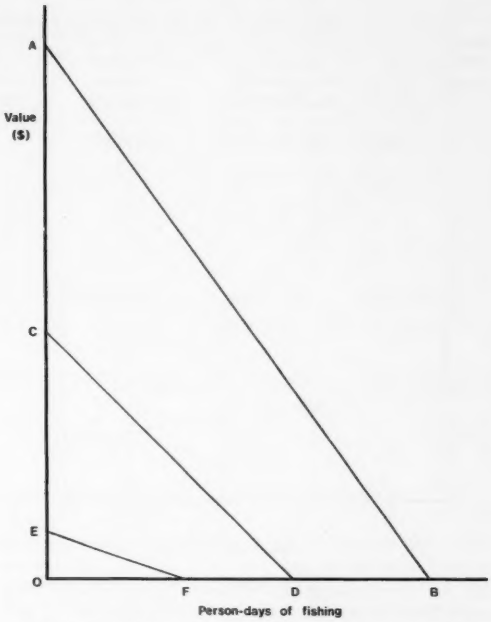

FIG. 2. Demand curves for sport fishing opportunities reflecting differences in the extent of available substitutes.

restriction of entry posed, the quantity OB would be taken or demanded by the users of the area.

The line AB is also the schedule showing at each point the amount that people would be prepared to pay for a day's access to this particular fishery, over and above all private expenditures on travel, equipment, and the like necessary to participate in the fishery. Thus, if entry were restricted to one unit (person-day) and priced at the level necessary to ration to this level, this one unit would be taken with a payment of OA. No one would be willing to pay more than this, and at a lower price more than one unit would be demanded. Similarly, at a level of use OB, no one would be willing to pay anything at all for additional opportunities in the fishery. The amount that could, in principle, be obtained for any intermediate unit of fishing opportunity taken is given by the corresponding point on the demand curve. The sum total of the amounts individuals are willing to pay for successive additions to fishing opportunities is measured by the area under the demand curve over the increment or range in question (Knetsch 1974; Mishan 1975).

Obviously, the shape and position of the demand curve, indicating the economic value of the resouce use, and therefore of the resource, will vary depending upon circumstances of the situation at hand. Usage levels will relate to the aggregate net value of a sport fishery in three significant ways. The higher the level of participation in the fishery, the greater the number of person-days of enjoyment taken, which will add to the aggregate net value of the fishery. On the other hand, the higher the number of participants, the greater the degree of crowding at the recreational site, which will tend to diminish the net value of each person-day of sport fishing. Also, the greater the extent of participation, the heavier the pressure on the fish stock and the lower the catch per person-day, which again will tend to diminish the net value of each person-day of fishing. It should be noted, incidentally, that for each level of demand, a constant level of resource availability over time is assumed. In other words, each level of demand is considered in the long term, matched by a corresponding sustainable catch level. Alternatively, the analysis could apply to a sport fishery that was annually restocked to the same level.

The definition of the resource itself will also be a determinant of the values at issue. For example, the demand curve representing the willingness to pay for opportunities to fish in the whole of the Canadian west coast fishery is certainly different from that for the Strait of Georgia. While demand curves are drawn in relation to specific sets of goods or services offered, it is generally the case that they vary in predictable fashion depending on the degree of substitution possible for the goods or services concerned. For example, in Fig. 2, AB might be taken to be the demand curve for all west coast salmon fishing. CD might express the willingness to pay for Strait of Georgia salmon fishing, and EF might be that for salmon fishing in a small area of the Strait. The latter curve is drawn lower to reflect the fact that there would be reasonably good substitutes for this resource service in the form of fishing in other areas, either adjacent in the Strait or elsewhere. And given the availability of ready substitutes people would be willing to pay relatively little for this particular service. It should be expected that the presence or absence

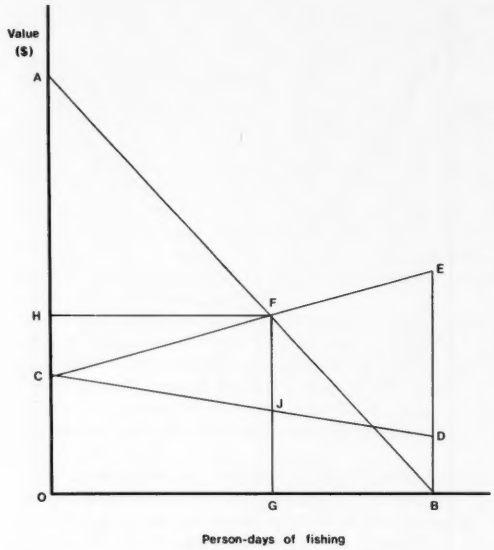

FIG. 3. The relationship of private and social benefits and costs in a recreational fishery with public resource ownership.

of other recreation opportunities or diversions would also affect the demand for a sports fishery. These effects, or really the cross-elasticities of demands, could be either positive or negative. While germane to planning and management, almost no work has been done on this important aspect of recreational demands.

Management of Recreational Fisheries

If no fee is charged nor other restriction to access applied, a sport fishery will be used to the maximum extent indicted by the demand curve concerned. In terms of Fig. 3, participants would put in OB person-days of fishing. The area ABO would then represent the net aggregate value of their participation as evaluated by them at their respective times of entry. However, this net aggregate of private values is likely to overstate the net aggregate social value of fishery participation at the level of OB person-days. The difference consists of two categories of social costs that are not part of private costs. First of all there may be various costs incurred by public authorities in providing access to recreational sites and in maintaining appropriate environmental conditions and facilities. These are shown in Fig. 3 by the area CDBO, assuming some decline in the cost per person-day of fishing at higher participation levels because of scale economies.

Secondly, there are "external diseconomies" to be considered, resulting from the "cost" that each additional participant imposes on the sport fishermen already committed to the fishery. In this connection it should be noted that the demand curve AB is so defined that it measures at each point the value of the fishery to the marginal entrant, assuming no further entry takes place (see legend to Fig. 1). But each time additional entry does take place there is a diminution in the value experienced by already committed fishermen, insofar as each additional participant will add to crowding and diminish the catch per fisherman. This "cost" or diminution of the aggregate value originally calculated for participants is shown by the area CED. It will tend to increase as the fishery expands in number of person-days, as each additional fisherman affects an increased number of already committed fishermen.

If free access to the fishery is maintained, so that private users put in OB person-days of fishing, the total social cost involved will be given by the area CEBO. The fishery then will be of net benefit to society only to the extent that the area ABO exceeds the area CEBO (or area AFC exceeds area FEB). It is apparent that the social cost of providing access for additional fishermen exceeds the net private benefits per person-day at participation levels beyond OG. In a sense then, any fishing beyond this level represents "overfishing," or a socially detrimental use of the resource.[3] The optimum participation level is OG, as it generates the largest possible aggregate net social benefit, viz. AFC. This participation presumably could be achieved if an access fee of FG per person-day of fishing were charged. Potential participants in the range GB would then not join in as the fee would be in excess of their willingness to pay for further use of the fishery. The understanding in expert circles that free access in sport fisheries is likely to lead to "overfishing," as it does in commercial fisheries, has been widely accepted in Europe and is gaining ground in North America despite public resistance to access fees.

On first consideration it would appear that the net social cost of allowing free access at OB person-days, instead of the optimal OG person-days, is given by the area FEB. By the same token one could say that this area measures the net income benefit of reducing effort from OB to OG person-days by imposition of a fee. However, there are also costs attached to enforcement and collection of access fees. If these costs exceed FEB, it would be socially preferable to allow free access to continue.

As will be discussed in a later section, there are other forms of access restriction that can be used in addition to pricing. A major advantage of price rationing, however, is that this selects in such a way as to assure that those valuing the opportunity the most, in terms of their willingness to pay, are those who gain access. Other methods would not assure such discrimination, and some who value the use of the site only slightly may obtain the opportunity over those who value it more dearly. A random distribution of admissions over the population at large perhaps would be the extreme case; but other schemes share this failing in large degree.

[3]The analysis here abstracts from the possible existence of hidden social benefits ("consumption external economies") from use of the resource between the participation levels of OG and OB. These would arise, for instance, if there were a positive social purpose to allowing participants in the range GB to participate, e.g. because society gains from the healthful circumstance of their participation beyond the private evaluations of the participants themselves (reducing public health care costs, reducing juvenile delinquency, etc).

TABLE 2. Characteristics of equilibrium levels of effort in a recreational fishery under different modes of access management

Form of access management	Categories of social benefits maximized	Incidental amounts of social benefit	Social benefits dissipated	Relation to socially optimum catch	Relation of access fee to social optimum	Relation to socially optimum level of effort
(A) Free access	—	Consumers' surplus	Resource rent	Indeterminate	Below optimum	Above optimum
(B) Public management for maximum net social benefits	Combined total of consumers' surplus and resource rent	—	—	Optimal	Optimal	Optimal
(C) Private owner managed access	Resource rent	Consumers' surplus	—	Indeterminate	Indeterminate	Indeterminate
(D) Restricted club member access	Combined total of resource rent and members' consumers' surplus	—	Nonmembers' consumers' surplus	Indeterminate	Not applicable	Below optimum

MODES OF ACCESS MANAGEMENT

It is possible with the aid of Fig. 3, to look at the generation of various net social benefits in recreational fisheries in the same fashion as was done for the commercial fisheries in Table 1. The results are summarized in Table 2.

When comparing commercial and recreational fisheries there is an asymmetry with respect to interacting interest groups. In commercial fisheries, fishermen-producers and fish buying consumers constitute distinctly separate groups with contrary interests in maximizing producers' surpluses and consumers' surpluses, respectively. In recreational fishing the consumer and producer functions are combined in the same group of people. Sport fishermen are consumers of the recreational opportunities provided, but they produce the recreational experience by their own activity. It is analytically more useful to consider sports fishermen simply as consumers, as the object of their activity is an enjoyable experience for which they are willing to pay. In seeking this enjoyment they will individually attempt to maximize their net benefits in the form of consumers' surplus.

In the analysis of recreational fisheries, therefore, consideration of producers and producers' surplus may be eliminated. In the absence of opposing groups of consumers and producers, there are no cases of consumers' monopsony and producers' monopoly to consider. However, there are two other forms of access control by special interest groups that may be applicable to a recreational fishery. One is the case of private ownership or control of the resource with management for private profit (case C in Table 2) and the other is the case of ownership or control of the resource by an exclusive group of consumers, i.e. a sport fishermen's club of limited membership (case D in Table 2).

PUBLIC AUTHORITY

Abstracting from the question of fee collection and enforcement costs (part of area CDBO in Fig. 3), maximization of net social benefits will occur where public management restricts participation (i.e. "fishing effort") to the level OG (Fig. 3). This is case B in Table 2, where an access fee (FG) is applied. A public authority could then collect a revenue of HFGO, which would be offset in part by public expenses of CJGO. With a fee of FG, the remainder (HFJC) after outlays have been subtracted is a sum collected by the public authority to assure optimal use. This is made necessary by the divergence of private marginal costs (which ignore congestion and stock reduction externalities) and social marginal costs.

The amount HFJC is in the nature of a resource rent collected by the public authority, representing society as the resource owner and manager. The rent could be used for the opening up of additional recreational fishing opportunities, considering the circumstances that the net public revenue was generated by fees collected from the sport fishing community. However, as the resource is owned by all of society and not just those using it for fishing, the fees might also accrue to the public treasury, which would avoid the inefficiencies inherent in earmarked funding.

Case B is considered "optimal," insofar as it achieves a maximum of the aggregate of possible net social benefits. As demonstrated above, this maximum is given by the area AFC. It is composed of the resource rent going to the public authority and of net benefits to sports fishermen. The latter are in the nature of a consumers' surplus that is measured by area AFH minus area CFJ. This latter area must be subtracted because it represents a double cost to participants — once as an access fee and once as a remaining loss owing to crowding and stock reduction even at this restricted use level (see above).

The implications of free access to a recreational fishery may now also be traced through case A in Table 2. There is no resource rent as the public authority manages the resource at a loss, collecting no revenue, while incurring costs equal to area CDBO. Sports fishermen, however, may enjoy a significant consumers' surplus, measured by area ABO minus area

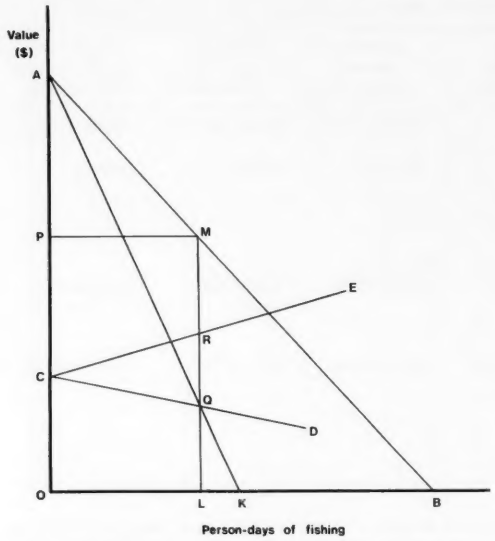

FIG. 4. The relationship of private and social benefits and costs in a recreational fishery with private resource ownership.

CED; the latter consisting of mutually imposed losses owing to crowding and catch reduction per person-day. The fishing effort applied under free access (OB) clearly is above the optimum (OG). However, it cannot be determined *a priori* whether the catch is above or below that achieved under optimal public management. A basic conclusion of the literature in fisheries bioeconomics is that a discrete increase in the level of effort may lead either to an increased or a decreased sustainable catch, depending on the biological dynamics of the stock and the particular levels of effort before and after the increase in question.

PRIVATE OWNER

Figure 4 illustrates the case of the private resource owner. Private operators controlling access rights on some stretches of New Brunswick and Quebec rivers provide an example. Conventional economic theory tells us that a private owner maximizing his returns would charge an access fee to sports fishermen users at such a rate that his marginal revenue would equal his marginal cost. His marginal revenue (AK) is determined by the location of the demand schedule (AB). His marginal cost schedule, consisting of amounts he would need to spend in maintaining the facilities of the fishery for successive increments in usage, is given by CD. Marginal revenue and marginal cost equate at a usage level of OL which will be obtained with an access fee of ML. Total revenue taken will then be PMLO, of which CQLO is absorbed by costs. The net return to the private owner, in the form of a resource rent, is PMQC, which is the largest rent that can be obtained by a uniform access fee, given the existing demand and cost schedules.

Sports fishermen users will enjoy some net benefits in the form of consumers' surplus. The demand curve indicates that their initial assessment of the value of the opportunity to fish is given by the area AMLO. However, of this they must surrender PMLO in access fees. Also, as explained earlier, crowding and stock reduction externalities must be taken into account.These are shown by schedule CE superimposed upon the resource owners cost schedule of CD. At a use level of OL, therefore, these crowding and stock reduction costs will be measured by area CRQ. In consequence, the only net benefit remaining to sports fishermen users is given by area AMP minus area CRQ.

It is not possible to say *a priori* whether the profit maximizing private owner will cause access fees, fishing effort, and related catches to be greater or smaller than those brought about by the net social benefit maximizing public authority. Both will take into account the cost of maintaining facilities (CD). On the benefit side, the public authority will be guided by consumer demand (AB), while the private resource owner will be guided by his marginal revenue (AK). The two schedules do have a fixed relationship. But in following the marginal revenue criterion the private owner will tend to restrict use of the resource by selecting a relatively high access fee. However, there is a countervailing factor in that the public authority will take into account the social costs implicit in crowding and stock reduction (CE), which are not of concern to the private resource owner. If these crowding and stock externalities are particularly large, they may cause the public authority to restrict access to a lower level for a given site than would the private operator. In Canada, as well as in other countries, we may observe an example of such a phenomenon in a related recreational field: compare the low density of camp sites in public camp grounds with the high density in private camping facilities.

PRIVATE CLUB

Finally, there is the case to consider of the private club that owns or controls a recreational fishery resource (case D). The members have a dual function as resource owners and consumers. The benefits accruing to them would consist of an indistinguishable combination of resource rent and members' consumers' surplus, but they would have to carry the cost of acquiring the resource and maintaining facilities. The situation is similar to that of a publicly managed fishery where all of society has "membership." But there is a difference in that a club would have an interest in restricting additional membership to protect their existing members from the increased costs of crowding and stock reduction that a growing membership would impose.

A limited growth in membership may be desirable from a club's standpoint if there are high initial costs of operation that can be spread over a larger intake of membership dues. Thus membership may be allowed to expand so long as average net benefits to members increase by expansion. This is illustrated in Fig. 5, where AB (the demand curve) represents marginal benefits and AT the corresponding average benefits. The marginal costs of operation are given by CD. Including the costs of crowding and stock reduction, marginal costs are given by CE and average costs by CS. Average net benefits

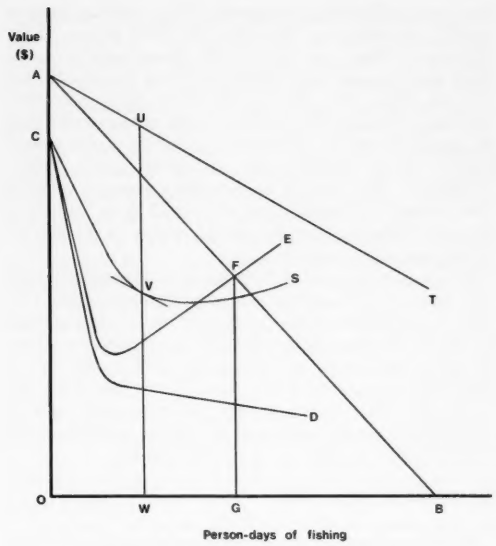

FIG. 5. The relationship of private and social benefits and costs in a recreational fishery with private club resource ownership.

are shown by the vertical distance between AT and CS, with a maximum of UV at a participation rate of OW. Optimum membership size is therefore the number corresponding to OW person-days of fishing. This user rate will be below the social optimum, which is OG at which marginal benefits to society (AB) equate with marginal costs (CE). The consumer's surplus that additional users in the range WG could have enjoyed will be dissipated.

Problems of Integrated Management

The practical problems of integrating management for commercial and recreational fisheries that exploit a common resource are complex. Many aspects are of a technical or biotechnical nature, involving such matters as gear conflicts, selectivity controls, seasonal closures, etc. In theoretical terms, the existing bioeconomic models for commercial fisheries analysis are not appropriate for application to the two fisheries combined. This is so largely because the relationship between catch size and net benefits in recreational fisheries is much more complex and quite different from what it is in commercial fisheries. McConnell and Sutinen (1979) have made a promising start in bioeconomic modeling of a combined commercial and recreational fishery. But as they have, for instance, ignored the crowding phenomenon in sport fishing, more work remains to be done in model development.

Granted that there are difficulties in model integration, some principles of joint management for the two fisheries may be firmly applied. Where the common goal is assumed to be the maximization of social benefits, the two fisheries will be at an optimizing equilibrium level of exploitation where marginal social cost equals demand in each fishery (see Fig. 3 and Copes 1972 regarding socially optimal equilibrium for recreational and commercial fisheries, respectively). Access fees, or other access restriction, in each fishery should be set so as to limit effort to the level that will meet this criterion. The difficulty in applying this rule will lie in devising calculations of the social costs that catches in one fishery impose on the other. In the case of the recreational fishery a rational approach may be to limit participation in the fishery on a double scale, one to control crowding and one to control catch levels.This could be done by charging a fee per person-day fishing as well as a fee per fish caught. The day fee would relate only to the crowding costs imposed on other sport fishermen, assuming that commercial fishermen are unaffected by crowding of recreational sites. The fee per fish would be calculated in relation to the stock reduction costs imposed on other recreational as well as commercial fishermen. This latter fee might be forgiven in sport fisheries when the fish are returned to the water unharmed after catching.

There may be good social reasons in either fishery not to control access solely by the magnitude of the access fee, even recognizing inefficiencies that may thereby be introduced. A desired level of fishing effort may be determined independently of actual fees charged, and access rights may be allocated by means other than fee charges. For instance, when dealing with economically distressed fishermen it may not be socially desirable to charge the full magnitude of effort-controlling fees, because of the implications in terms of distributional equity. Allocation of access in such cases may be by fiat of the management authority (e.g. on the basis of social criteria) and at little or no monetary charge. It may be noted that in recreational fisheries, too, access control and allocation may be by means other than fee charges. For some New Brunswick rivers recreational salmon licences are distributed by lottery (though nominal fees below an optimizing level are collected in addition).

Different fee levels may be appropriate where the social benefits of access are in different categories. The practice of charging nonresidents higher fees than residents may make sense from the standpoint of a public authority that is trying to maximize local benefits. It will charge residents low fees so that they may participate at a high level and gain much consumers' surplus of benefit to the local society. But if the public authority is not particularly concerned with the welfare (consumers' surplus) of outsiders it will try to extract the greatest possible resource rent from them by charging them higher license fees.

Measurement of Welfare Effects

The design of improved management strategies for a recreational fishery is dependent, in no small part, on the availability of estimates of the values that may be generated. Given the present paucity of data, even crude estimates may assist in improving management decisions. But if these decisions are to be made with confidence, greater precision is required in estimating recreational fisheries values. The measurement problem is not one solely of technique or method, although this is important. The problem is compounded by the existence of alternative measures of consumers' surplus values. This is particularly a concern in cases

of large (nonincremental) changes, such as the allocation or reallocation of resources between fisheries and other uses.

Alternative Benefit Measures

The economic value of a commodity or service is normally taken to be the amount which users are willing to pay to obtain the right to it. However, there may be instances, and the case of sport fisheries may be among them, where an alternative concept of value will be more appropriate. That alternative concept is the amount of money which people would require in compensation for giving up the right to a commodity or service which they previously enjoyed.

Empirical estimates that have been made suggest that the alternative values ascribed to a resource according to the two different concepts may vary considerably. When people are asked what is the minimum amount which they would accept as compensation for foregoing the rights to the use of a fishery resource, a far larger value is usually reported than when they are asked how much they would pay to maintain access to the same resource. There are a number of reasons for this divergence of value estimates. The limitations of survey techniques and the hypothetical nature of the questions put, no doubt, are partly responsible.

The most common explanations offered by economists for this response variation have centered on two issues. The first is that an income constraint operates in the case of one measure and does not in the case of the other (Krutilla and Fisher 1975). The amount which an individual can or will pay for anything is limited by his income. But there is no income constraint when a respondent is asked to quote a figure for a minimum compensation acceptable to him.

While the income constraint argument may be important in the case of some individuals for certain kinds of goods or services, this provides but a partial explanation. Income constraint would not be a significant factor in the case of goods and services that make up but a small part of income expenditures. For many, if not most recreational fisheries issues, this latter situation is likely to be the rule.

The second explanation which has been offered is that of the difference between the "compensating variation" measure of consumers' surplus and the "equivalent variation" measure, related to people's changed relative preferences at different income levels. The distinction between the two measures rests on the circumstance that there may be a significant difference in real income with and without access to a fishery (Mishan 1975). This explanation too is but a partial one. Having or not having access to a fishery is not likely to be very important to most individuals, so that the income effect of sport fishery access probably will be modest.

A more plausible explanation, perhaps, is that people place a lower value on "opportunity cost" income — money that they can receive but do not have, than on realized income — money that they have and must "dig into their pockets to spend" (Thaler 1980). Consequently, more opportunity cost dollars, those not yet received must be paid to obtain agreement to give up something, than would be paid out of realized dollars to retain access.

Whatever the reason for the observed response differences in the case of the two measures of value, there are considerations that indicate the appropriate choice between them in specific circumstances. Basically, the choice hinges on the direction of change, i.e. whether the change adds to or subtracts from current levels of welfare of the persons affected (Knetsch 1980). Thus, the measure of how much individuals would be willing to pay would be in order in cases concerning the acquisition of an entitlement or privilege to a new sport fishery or an improvement in current sport fishery "holdings." The onus of demonstrating superior value in sport fishing use would seem to be with those desiring a changed allocation, and this would appear to suggest the willingness to pay measure.

The measure of value of the required compensation, on the other hand, might be viewed as appropriate when dealing with cases involving the giving up of rights to an existing sport fishery or involving the diminution of its productivity. Here the value would seem to be best measured by the loss of welfare of current sport fishery users. Proponents of a hydro facility that would destroy or severely damage a sport fishery, for example, should measure their liability in terms of the amount needed to compensate sports fishermen.

Measurement Methods

Attempts to measure the economic value of the sport fishery services of resources have been relatively few in number and not always notable for their appropriateness. This reflects both lack of attention and difficulty. The generic problem is that no direct measures are available of the values sought. Some isolated instances of a market or market-like measures exist. But these are rather rare and not capable of being readily generalized to other circumstances. Often they concern prices for a bundle of services that include the services of the fishery resource among other joint offerings. More effort seems warranted on the collection and analysis of whatever direct evidence exists on prices being paid for sport fishing. However, as a practical matter, it appears necessary also to develop some appropriate indirect measures of sport fishery values.

One early proposal for obtaining a surrogate measure centered on the commercial value of the fish caught in the course of fishing for recreation. The major conceptual problem here is that this measure fails to take account of the primary service of the resource, viz. the activity of fishing. As a recreational pursuit it is indeed of value to be able to fish, even if on occasion or most often, to do so unsuccessfully.

Another proposal which has been taken far more seriously than most, even though it appears no more appropriate, is the so-called expenditure method. Briefly, the notion here is that the value of fishing is given by the expenditures of people engaging in it — for equipment, bait, travel, lodging, food, and drink. The rationale is that if fishing were not worth this much to people, they would not have put forth these outlays to enjoy it. The difficulty is that the real measure needed is one of how much they would spend over and above the outlays mentioned, that is for the use of the resource. While of little utility as a measure of the value of sport fishery resources, the large numbers generated by expenditure surveys have often excited public officials into repetition of such surveys.

There are two general approaches which have been used

with more effect and which have gained reasonable respect and creditibility. The first consists of surveying the sport fishing population and asking respondents for a direct measure of the value they receive. The second involves the imputation of a demand curve and willingness to pay measure from travel cost data pertaining to the use of existing fishery resources. The latter approach, of course, is only appropriate in cases where the willingness to pay measure should be used rather than the compensation demanded measure. The former approach may be used for either measure.

Questioning of participants in various recreational activities has been used from time to time as a direct means of assessing the value which these people place on the opportunity to enjoy such pursuits. One of the earliest and most widely cited is the work of Davis (1964; Knetsch and Davis 1966), in which he used the method to measure the value of the recreational use of wilderness-like areas in Maine. He used a bidding game on the site to establish an upper bound to what people would have paid to enter the area. The method should, in principle, yield a valid measure of the recreational willingness to pay value of the resource. In practice, problems of interview bias and the difficulty of generalizing the results to other areas have posed major problems.

Hammack and Brown (1974) used a mail questionnaire of hunters to establish a value for wildlife resources. Their effort was notable in part because of the attempt to estimate both a willingness to pay measure and a required compensation measure of value. While questions can perhaps be raised concerning the definition of the resource that people thought was at issue, it is interesting to note that in terms of the median values obtained, the stated requirement for compensation to forego use of the resources was four times the indicated willingness to pay to preserve it on the part of the then current users.

More ambitious efforts to use direct interview responses to measure fishery values have been undertaken by the Pacific Region personnel of Fisheries and Oceans Canada. On the whole these appear promising, although it is not yet clear how the results can be used to measure values that would be associated with anticipated changes in resource commitments — fishery enhancement, destruction of a fishery, or a major change in the circumstances of a substitute area.

The travel cost method of imputing value has now been extensively used for estimating values of a variety of recreational assets. Most have been parks or recreational areas (Knetsch 1974), although values of sport fishing have also been successfully measured (Brown et al. 1964). Generally, however, the method is site-specific and of limited use for evaluation of regional fishery assets.

Conclusion

Pressure on the world's fish stocks escalated seriously in recent decades. Physical depletion of many stocks and declining economic returns have spurred governments to action. The evidence of serious overfishing has been used by coastal states as a justification for the imposition of 200-mile fishing limits. Increasingly, fisheries around the world are being brought under limited entry management regimes.

In the meantime, the demand for recreational fishing opportunities has been increasing rapidly as a result of population growth and, in many instances, increasing affluence. With escalating pressure on recreational fishery resources, the need for effort restriction in the more heavily exploited sport fisheries is now also becoming increasingly apparent. Rational management is required if social benefits from recreational fisheries resources are to be protected and enhanced. The challenge now is to sharpen analytical insights, to increase knowledge of the available resources and the potential demands thereon, and to develop facility with sophisticated management techniques that will allow for better utilization of recreational fishery resources.

There are many areas in which additional analytical work is required. A better understanding is needed of the complexities of integrated management of commercial and recreational fisheries where they utilize a common resource. On the side of commercial fisheries analysis, the preoccupation with resource rent maximization to the neglect of consumers' and producers' surplus needs to be overcome. For the latter, two net benefits are of preeminent importance when recreational fishery values must be taken into account.

On the side of sport fisheries analysis, the complicated link between the recreational benefits generated and the amount of the resource used needs to be explored and defined with greater clarity. Competition with the commercial fishery is in terms of the amount of the resource used. But the rival pressures on the resource may be lessened by concentrating on alternative value aspects of the sport fishery concerned with the quality of the recreational experience. Such factors as environmental appeal and lack of site crowding are often more important than the amount of fish caught.

The time appears ripe for a major effort to correct the past neglect of recreational fisheries analysis.

Acknowledgments

The authors are pleased to recognize the stimulation, encouragement, assistance, and advice received from A. L. W. Tuomi. As Director of the Recreational Fisheries Branch of Environment Canada, he arranged for the authors to present the key paper at the 1976 Canadian Sports Fisheries Conference, of which the present article is an extensively revised and retitled version.

Generous financial support, first from Environment Canada, and latterly from the Social Sciences and Humanities Research Council of Canada, is gratefully acknowledged.

Helpful comments received from referees have been much appreciated by the authors.

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The Thermodynamic Origin of Ecosystems

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JOHNSON, L. 1981. The thermodynamic origin of ecosystems. Can. J. Fish. Aquat. Sci. 38: 571–590.

A general theory of the origin of ecosystems in thermodynamic terms is developed. Regular fluctuations in the availablility of energy give rise to dissipative structures in systems where the boundary constraints preclude the development of the equilibrium state. Dissipative structures are patterns in the energy flow that cease to exist when the energy flow ceases; when in the vicinity of their equilibrium position, they tend to a state of least entropy production. The ecodeme, or group of like individuals interacting equally within the constraints of the niche boundaries, exhibits the characteristics of a dissipative structure. The characteristics of a dissipative structure demand that it actively acquire and conserve energy, and that it exhibit organization. Organization implies the existence of order and a goal or end point; order is represented by uniformity of individuals in the ecodeme, the goal is represented by the state of least entropy production. Within the ecosystem ecodemes interact so that the system as a whole tends to proceed to a state of maximum entropy and maximum entropy production rate. In this way the ecosystem functions as a series of coupled shock absorbers and tends to assume a state of maximum steadiness or least oscillation. The condition of least entropy production and least oscillation can be most clearly recognized in the dominant species at the climax in an autonomous system. An autonomous system is one that approaches the closed thermodynamic condition. The biosystem or total biological complex within the biosphere, being completely autonomous, tends towards a state of maximum steadiness within the constraints of the energy input regime. Migration patterns thus develop in response to the reduction of local instabilities caused by local differences in energy input.

As organisms develop in response to fluctuations in energy availability, greatest diversity exists where the excitation of the system is most heterogeneous. Heterogeneity of excitation develops in environmental conditions that tend to be most homogeneous in their overall pattern. The more homogeneous and the greater the total amount of energy available annually, the greater the capacity to break up into a large number of minor fluctuations under the influence of the trend to increased entropy. Heterogeneity is developed under the influence of daily changes in availability and the development of physical structure in the ecosystem. Maximum diversity, therefore, is attained in those geographical regions in which wet tropical forest develops. As the heterogeneity of the overall climatic pattern increases and total energy available decreases with increasing latitude, so diversity tends to be reduced, and individual biomass, relative to input, increases.

Evolution results from continuous self-acceleration of the energy flow under conditions of constant energy input. Self-acceleration results from the tendency towards ever-increasing dispersal of the energy within the ecosystem as expressed in ever-increasing diversity; increasing diversity causes an increase in the rate of energy flow. Under these circumstances the energy flow to each ecodeme tends to become attenuated so that there is selection for improved energy acquisition to maintain a satisfactory solution to the acquisition–conservation integral. This increase in acquisitive capacity demands an increase in complexity and a further increase in rate of energy flow.

These concepts, by way of validation, are examined in the context of stability, energy transfer, natural selection, fitness, and the observable characteristics of evolution.

Key words: thermodynamics, ecosystem, energy flow, dissipative structure, ecodeme, organization, order, diversity, stability, energy transfer, fitness, reproduction, group selection, natural selection, evolution

JOHNSON, L. 1981. The thermodynamic origin of ecosystems. Can. J. Fish. Aquat. Sci. 38: 571–590.

Dans l'article qui suit, l'auteur expose une théorie générale de l'origine des écosystèmes en termes thermodynamiques. Les fluctuations régulières de disponibilité d'énergie donnent

Printed in Canada (J5952)
Imprimé au Canada (J5952)

naissance à des structures dissipatrices dans les systèmes où les contraintes des couches limites empêchent un état d'équilibre de s'établir. Ces structures dissipatrices sont les caractéristiques du flux énergétique qui disparaissent quand disparaît le flux énergétique lui-même. Lorsqu'elles sont proches de l'équilibre, ces structures tendent vers un état de production de moindre entropie. L'écodème, ou groupe d'individus semblables agissant les uns sur les autres dans les limites imposées par les frontières des niches, exhibe les caractéristiques d'une structure dissipatrice. Cette dernière, par définition, doit acquérir activement et conserver l'énergie, et doit de plus être organisée. L'organisation implique un ordre et un but ou point d'arrivée; l'uniformité des individus dans l'écodème représente l'ordre, et l'état de production de moindre entropie représente le but. Au sein de l'écosystème, les écodèmes interagissent de telle manière que l'ensemble du système tend vers un état d'entropie maximale et un taux de production d'entropie maximale. L'écosystème fonctionne donc comme une série d'amortisseurs de chocs couplés et tend à adopter un état de stabilité maximale ou de moindre oscillation. Cette condition de production de moindre entropie et de moindre oscillation se reconnaît le plus facilement à l'espèce dominante au stade climacique d'un système autonome. Un système autonome est celui qui se rapproche de la condition thermodynamique fermée. Le biosystème, ou complexe biologique total au sein de la biosphère, étant complètement autonome, tend vers un état de stabilité maximale dans les limites du régime d'entrées énergétiques. En réponse à la réduction des instabilités locales causées par des différences locales d'entrées énergétiques, il se développe diverses modalités de migration.

Comme les organismes se développent en réponse à des fluctuations de disponibilité d'énergie, on observe la plus grande diversité là où l'excitation du système est la plus hétérogène. Il y a hétérogénéité d'excitation dans des conditions ambiantes qui tendent, dans l'ensemble, à être le plus homogènes. Plus la quantité totale d'énergie disponible annuellement est homogène et plus elle est grande, plus grande est la capacité de résolution d'un grand nombre de fluctuations mineures sous l'influence de la tendance vers une entropie accrue. L'hétérogénéité résulte de l'influence des changements quotidiens de disponibilité et du développement de la structure physique dans l'écosystème. C'est pour cela qu'il y a diversité maximale dans les régions géographiques où évolue une forêt tropicale humide. Étant donné que l'hétérogénéité des caractéristiques climatiques générales augmente et que l'énergie totale disponible diminue avec une élévation de latitude, la diversité tend à diminuer, et la biomasse individuelle, par rapport aux entrées, augmente.

L'évolution est le résultat d'une auto-accélération continue du flux énergétique dans des conditions d'entrées énergétiques constantes. L'auto-accélération résulte de la tendance vers une dispersion sans cesse croissante de l'énergie à l'intérieur de l'écosystème et exprimée comme diversité sans cesse croissante; un accroissement de diversité entraîne l'accroissement du taux de flux énergétique. Dans ces circonstances, le flux énergétique vers chaque écodème tend à s'atténuer, de sorte qu'il y a sélection vers une meilleure acquisition de l'énergie afin de maintenir une solution satisfaisante à l'intégrale acquisition−conservation. Cette augmentation de capacité d'acquisition exige une complexité accrue et une augmentation supplémentaire du taux de flux énergétique.

Comme vérification, l'auteur examine ces concepts en termes de stabilité, de transfert énergétique, de sélection naturelle, d'adaptation et de caractéristiques observables d'évolution.

Received February 1, 1980
Accepted January 22, 1981

Reçu le 1 février 1980
Accepté le 22 janvier 1981

For even those (animals) that are not attractive to the senses, yet to the intellect the craftmanship of nature provides extraordinary pleasure for those who can recognise causes in things and who are naturally inclined to philosophy

ARISTOTLE
de partibus Animalium

Application of the established laws of thermodynamic to biological systems has occupied a central position in the minds of biologists for many years (Brillouin 1949; Odum 1969; Monod 1971; Gallucci 1973), but the formulation of a coherent theory, applicable to all aspects of the problem, has proved extremely difficult. These difficulties seem to arise primarily from the extreme complexity of ecosystems, combined with the high degree of variability that tends to obscure recognition of the emergent properties. But it appears that the enigma has been compounded by the attempt to apply classical equilibrium thermodynamics to nonequilibrium situations.

Nonequilibrium thermodynamics as developed by Prigogine (1978) and his associates (Glansdorf and Prigogine 1971; Nicolis and Prigogine 1977) introduces new concepts and new structures that seem to be fundamental to understand-

ing the role of thermodynamics in biological applications. The new concepts are largely concerned with time; the new structures arise as patterns in the energy flow and disintegrate when the flow ceases.

Equilibrium theory is centered on the concept of an isolated system coming to a unique equilibrium state, a state of no change, in which there is no exchange of energy or matter with the external world. This may be constrasted with a closed system in which there is exchange of energy with the external world but no exchange of matter, and an open system in which both energy and matter are exchanged. Nonequilibrium systems obey the same basic laws as equilibrium systems, but they can exist only where the boundary constraints are such as to preclude the establishment of equilibrium; they can thus only exist as closed or open systems. In this paper I have attempted to interpret the macroscopic phenomena of ecosystem functioning in terms of nonequilibrium theory.

The ideas to be discussed were originally stimulated by what appeared to be anomalies in the data obtained during many years of investigation of lakes in Arctic Canada. These lakes are all of comparatively recent origin, having been formed between 8000 and 10 000 yr BP, during the most recent retreat of the Laurentides ice cap. In the present context their most important attributes are (1) since their formation they have been entirely free from human interference, enabling them to proceed to the limits of their potential capacity, (2) they are essentially self-contained except where clearly identifiable migratory stocks exist, and (3) the ecosystems supported by these lakes are comparatively simple.

For between 8 and 11 mo of the year these lakes function as closed ecosystems sequestered from the external world by a layer of ice 2–3 m thick; the only energy entering is a small fraction of the external light, and the only energy leaving does so in the form of heat. For the remainder of the year, during the short open-water period, exchange of biomatter is confined to the emergence of aquatic insects and the activities of a comparatively small number of fishing birds. Primary production is extremely low (Kalff 1970; Hobie 1973; Kalff and Welch 1974; Welch and Kalff 1974) and energy input is variable owing to differences in the date of loss of ice cover. In an early year the lakes are not free of ice until about a month after the summer solstice; if the season is late ice may linger until the 1st week in August.

In spite of low energy input, fish stocks are abundant and biomass is high (Hunter 1970; Rigler 1975; Johnson 1980). The major stocks in these lakes are Arctic charr, *Salvelinus alpinus*, lake charr (lake trout), *S. namaycush*, lake whitefish, *Coregonus clupeaformis*, and two to three species of cisco, *Coregonus* spp.

Two major anomalies, at least with respect to theory current at the start of the investigations, were soon apparent in the data obtained from the study of the fish stocks. In the first instance, very similar, bell-shaped, catch curves, covering essentially the same range of fish sizes, were obtained when the length distribution of the individual catches from a wide range of mesh sizes was plotted (Johnson 1972, 1976). When the catch curve for the combined catch was plotted, it differed very little from that of the individual mesh sizes. These results were repeated from lake to lake and covered a wide range of mean size. The curves obtained had the general shape of a normal distribution, but values tended to be more highly clustered around the modal size than might be expected. The invariability of this pattern of distribution indicated, most strongly, that it was a real characteristic of a fish stock in an undisturbed state and could not be attributed to an artifact of the sampling procedure.

In conventional fish population dynamics theory (Ricker 1975; Beverton and Holt 1957), growth of a population occurs at a set rate, although exhibiting considerable individual variation; it is generally quite rapid at the start but decreases regularly with increasing age. Such a regular pattern of growth gives rise to a size distribution in which numbers in each length-class decrease exponentially as length increases; length and age are, in fact, considered to be strongly correlated. The length distribution is therefore considered to be comparable with the negative exponential curve that describes the number of fish in a single age cohort, at each age, throughout the life of that cohort. In reality, catch curves almost invariably show length distributions that are bell-shaped. This is usually attributed to gear selection, the seclusion of younger (smaller) fish on nursery grounds inaccessible to the fishery, and the process of 'piling-up' (Baranov 1918). Piling-up is ascribed to a slowing down in growth rate with increasing size, so that more fish grow into a given length interval than grow out of it in the same time period.

In the lakes sampled the 'piling-up' process could not be attributed to a regular growth pattern since individiuals of modal length invariably displayed a great range in age; frequently the modal length group contained representatives of all age-groups in the main body of the catch: fish of identical size might be separated by as much as 10–12 yr in age (Fig. 1).

The other anomaly was that these stocks invariably exhibited great age and size, manifesting all the characteristics of continuity and stability in the face of the variable Arctic environment. This continuity of the major vertebrate in the ecosystem was in strong contrast with the small mammal stocks of the surrounding terrestrial systems, whose oscillations gave rise to the belief that simple systems are unstable and hence occupied a polar position in the diversity–stability hypothesis (Elton 1924, 1927, 1958; Elton and Nicholson 1942; MacArthur 1955).

The fish stocks in these untouched Arctic lakes were recognized as having a structure very similar to that of the dominant tree species in a climax forest (Johnson 1976), giving rise to the conclusion that the lakes in question had also reached a climax, in all significant ways, comparable with the climax of vegetational theory (Jones 1945; Whittaker 1951, 1953; Langford and Buell 1969; Whittaker and Woodwell 1972). In both the forest system and the Arctic lake the dominant species is recognizable by its high biomass, large individual size, uniformity in size, considerable age (although with only a very loose correlation between age and size), and a low level of recruitment stock.

These observations led to the initiation of a series of whole lake experiments designed to explore the situation in greater depth. These experiments were all conducted on small Arctic lakes (7–60 ha) of comparatively simple structure; in each case the only fish species present was Arctic charr; all the lakes were free from human influence and the stocks were completely nonmigratory or landlocked. Holling (1973) suggested that if such lakes could be found, they might provide

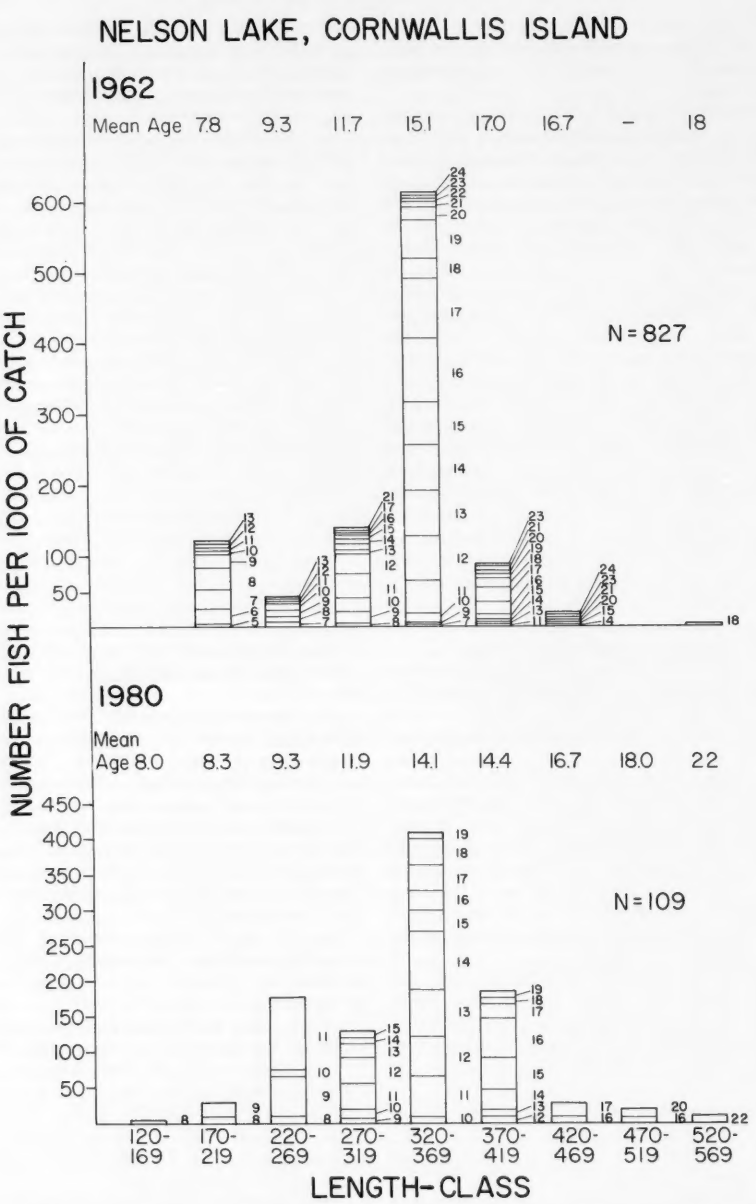

FIG. 1. Length–frequency histogram, showing proportional age composition within each 50-mm length-class, of catches of Arctic charr, *Salvelinus alpinus*, from Nelson Lake (74°42′N; 94°14′W) Cornwallis Island, N.W.T. These samples collected at an interval of 18 yr show a remarkably high degree of constancy: continual maintenance, in the undisturbed condition, of a highly developed *K*-configuration. The data in the upper panel were collected by A. W. Mansfield of the Arctic Biological Station, Ste. Anne de Bellevue, in 1962; those in the lower panel by Bruce Stewart and Gary MacDonald of the Freshwater Institute, Winnipeg.

a real and valuable facility against which to test theory.

In all cases except one, the general bell-shaped, length–frequency, distribution curve was obtained, although intensive efforts were made to eliminate gear selection; the exception provided striking confirmation of the basic hypothesis (Johnson 1981). It was further found that this unimodal type of distribution curve was retained even when a drastic reduction in stock was effected. In unexploited lakes the same bell-shaped length distribution remains constant over time with a remarkable degree of fidelity (Fig. 2).

The most significant result from these investigations is the inescapable fact that the charr stock, as a whole, behaves as a coherent unit and in this way demonstrates the existence of organization. As elucidated by Pittendrigh (see Mayr 1976), organization is used in the strict sense of implying both order and the tendency to proceed towards a goal. Order is recognizable by the uniformity in the size of the stock, goal-directedness by the capacity of the system to retain, or regain after perturbation, a unique ground state. The existence of a strong damping mechanism, reducing oscillations in stock abundance, is taken as evidence of the existence of organization in its functional role. Damping is effected through a time delay on the energy flow in combination with goal-seeking behavior. The characteristics of a well-damped system are exemplified by the uniformity and continuity exhibited by the Nelson Lake stock of Arctic charr over a period of 18 years.

From the results of these investigations it was concluded that the limits to size distribution in any stock can be represented by two curves (Fig. 2). The curve in the upper panel represents the size distribution when the energy flow reaches the maximum value attainable; in the lower panel the time delay in energy flow reaches a maximum value, resulting in piling-up at a specific size, but a size that is not closely related to age. This distribution is characteristic of a stock of organisms that achieve considerable age and is of determinate growth pattern, for example, a human population, where adult density is kept at a constant level, and where juvenile stock and recruitment closely approximate the needs of replacement. It also appears to be characteristic of organisms of indeterminate growth pattern, such as fish or trees, living within the constraints of a closed ecosystem. These two curves represent the conditions in which *r*- and *K*-selection are favored (MacArthur and Wilson 1967; Pianka 1970); they may be designated *r*- and *K*-configurations, respectively. The *K*-configuration is characteristic of the dominant species in crowded, climax conditions where turnover time has increased to its maximum value, whereas *r*-selection is characteristic of organisms adapted to high turnover rates and high levels of oscillation in abundance. When a stock in the *K*-configuration is exploited, the energy flow rate increases and it tends to move in the direction of the *r*-configuration and more rapid energy flow. In the undisturbed state organisms in the *r*-configuration will be those adapted to rapid energy accumulation and high mortality rates resulting in frequent oscillation in abundance; even under these circumstances it is unlikely that the *r*-configuration will ever be more than a state to be approached, seldom being realized.

If each ecodeme within a virtually closed system exhibits organization, then the ecosystem as a whole will function as a series of coupled shock absorbers; at each level in the trophic hierarchy the fluctuations will be reduced until a state of least fluctuation is achieved by the dominant at the climax. In a small Arctic lake approaching a closed system, the algal primary producers will fluctuate greatly in abundance in response to the seasonally changing energy inputs and the grazing pressure; at each trophic level the fluctuation is reduced until the dominant fish species is reached and fluctuations are largely eliminated. The dominant species is therefore the one best able to integrate energy acquisition and conservation.

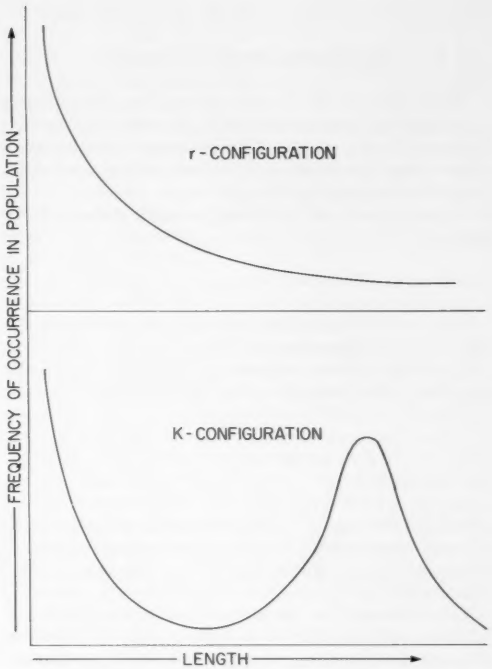

FIG. 2. Generalized representation of length–frequency distributions of organisms growing under different ecological conditions. The upper panel represents the size distribution where energy flow is at a maximum rate, the *r*-configuration in which *r*-selection is induced. The lower panel represents the size distribution in a system adjusted to minimum energy flow rates: the *K*-configuration in which *K*-selection operates.

The actual level of oscillation or degree of steadiness achieved by a system under such conditions will be dependent on the annual regularity of the energy input, both with respect to timing and total quantity, as well as the individual nature of the species present. It is not to be expected that the ecosystem at the climax will exhibit a rigid architecture; there is a continuous interplay of factors as energy values change within season, between seasons, and over longer secular periods. The truly steady state is an ideal, likely to be achieved only under a very regular input regime. In view of the variables and the vagaries of climate, it is perhaps surprising that the fish stocks exhibit the high degree of steadiness

and continuity that they actually do.

Equilibrium Thermodynamics

Thermodynamic theory states that of all the allowed states in an isolated system, there is one, and only one, that is a stable equilibrium state; from this it follows that the entropy of an isolated system increases monotonically until it reaches a maximum value at equilibrium.

The entropy, S, of a system is usually defined by the equation:

$$(1) \quad F = E - TS$$

where F is the Helmholts free energy, E is the internal energy, and T is the absolute temperature.

It is also possible to define entropy in terms of probability according to the Maxwell–Boltzmann equation:

$$(2) \quad S = -k \sum_{i=1}^{i=n} Pi \log Pi$$

where $\Sigma Pi = 1$ and Pi is the probablility of an idealized physical system being in the state of i of n possible equivalent states, and k is the Boltzmann constant (Woolhouse 1967; Wilson 1968).

This implies that in the thermodynamic description of a system, a large number of alternative states or alternative pathways for the energy is equivalent to high entropy; a system will tend to enter and remain in that high set of alternative states (Goodman 1975). Thus energy entering a system will tend to follow the maximum number of pathways available to it; the higher the number of pathways the greater will be the entropy since a large number of pathways denotes a tendency towards random distribution of the energy ($Pi \rightarrow 0$) and few pathways implies order ($Pi \rightarrow 1$).

Entropy increases when the ordered energy in light waves is transformed into increased random molecular activity; this may be recognized as an increase in temperature of an object placed in a light path. This process is irreversible and only irreversible processes contribute to an increase in entropy. During the transformation from light to heat, work may be done as a result of irreversible processes, giving rise to a temporary, or more or less permanent, increase in order; when incapable of further work, the energy is dissipated as heat. In a closed system that has reached a steady state, the rate at which energy is assimilated is equal to the rate at which it is dissipated as heat.

Time does not enter into the basic thermodynamic laws since they are concerned with quantity of energy and its distribution. However, as Prigogine (1978) points out, time does feature in a very specific and one-sided way. As time is used to measure the rate at which change occurs, it is associated with changes that lead to the equilibrium state, but when equilibrium is reached, time essentially ceases to exist since equilibrium is defined as a state of no change.

Nonequilibrium Thermodynamics

Largely as a resuslt of the work of Prigogine and his associates, new developments have taken place in the analysis of systems in which boundary constraints are such as to preclude the attainment of equilibrium. Nonequilibrium implies a continuous exchange of energy and entropy with the external world. Under the appropriate circumstances nonequilibrium can be a source of order giving rise to new dynamic states known as *dissipative structures*. Dissipative structures arise as a result of irreversible processes; they can only exist in conditions of continuous but fluctuating energy flow, and in conditions where the physical and chemical characteristics of the system allow fluid adaptation. Prigogine (1978) states succinctly "...the order created in these unstable but coherent dissipative structures has three aspects that are always linked together: firstly there is the function as expressed in the chemical equations, secondly the space–time structure resulting from the instabilities, and thirdly there are the fluctuations that are the basic trigger of the instabilities." Dissipative structures can therefore arise only in nonequilibrium systems as patterns in the energy flow; they can exist only where the system is capable of fluid internal change and adaption within certain boundary conditions; they can survive only in the maintenance of the flow pattern.

Prigogine (1978) emphasizes that in considering dissipative structures new theoretical structures arise "...in which time appears with its full meaning associated with irreversibility or even with "history" and not merely as a geometric parameter associated with motion."

A theorem of fundamental importance derived by Prigogine (1978) is that a dissipative structure in the vicinity of its equilibrium tends to assume a steady state in which the rate of entropy production reaches a minimum value. That is, when the boundary conditions prevent the attainment of equilibriuim (zero S production), the system settles down to a state of *least dissipation*. Least dissipation represents the least rate of entropy production relative to the energy accumulated in the system; least dissipation occurs when the energy flow rate through the system is at a minimum value for the existing constraints; and it implies that maximum time delay has been imposed on the energy flow. Least dissipation therefore represents an inertial property of the system. When such a system is perturbed, the rate of entropy production increases, but the system reacts by coming back to a minimum value for S production. Far from equilibrium, Prigogine found, somewhat to his surprise, that although the conditions of equilibrium are universal, the thermodynamic behavior of dissipative structures could be quite specific, even opposite to that indicated by the theorem of least entropy production.

A dissipative structure cannot be regarded merely as a passive receptor of energy; energy must be actively acquired through the maintenance of a negative potential with respect to the external world. This may be compared with the formation of a crystal. In crystal formation a group of molecules in appropriate juxtaposition and in the appropriate environment transfers heat energy to the external world. When the necessary quanta of energy have been transferred and the system reaches a threshold value, the molecules cohere in an ordered way and crystallization takes place; equilibrium has been reached and no further change occurs. In the formation of a dissipative structure the component elements may be regarded as remaining in a state of incipient crystallization where order is created, but without equilibrium being reached. As bound-

ary conditions preclude the formation of equilibrium, energy continues to be acquired at a more rapid rate than that at which it is dissipated until a steady state is reached, the energy accumulation is greatest for the prevailing conditions, and assimilation and dissipation of energy are equal.

The introduction of a new element into a system may endow it with new properties that are, in themselves, not deducible from the laws governing the original system, but at the same time there is no implication that the original laws are being contravened. As stressed by Lorenz (1973), when discussing Hartmann's scheme of philosophy in relation to levels of phylogenetic complexity, B is never non-A but always A + B. In this way the concept of nonequilibrium does not contravene the laws established for the equilibrium system, but neither is it possible to predict the outcome of events at the higher, more inclusive, level from the original set of laws. To invert Lorenz's statement (p. 39), the coming into existence of life itself is basically of the same nature as each step in phylogeny that leads from a creature of lower to one of a higher order.

Prigogine and Waime (1946) recognized some considerable time ago that living organisms exhibit many features characteristic of a dissipative structure. Apart from the fact that they must consume energy continuously to remain alive and maintain a specific pattern in the energy flow, a clearly recognizable feature is the tendency to attain a state of least entropy production over their period of development. This is apparent in the reduction of metabolic rate over development time. At maturity an organism enters a steady state during which phase a perturbation (such as a wound being inflicted) causes an increase in metabolic rate; when the perturbation ceases metabolism returns, once more, to the initial ground state. If the perturbation continues, a steady state is achieved at a new level, in which entropy production is least for the new conditions.

The relationship of an organism to time, in its full historical implication, is clearly apparent in its evolution and also in its ontogeny. A mature organism represents the end product of a historical process that began when life first appeared — within the genome of each organism there is the accumulation of some 2.5 billion years of experience and this experience is translated into current actuality through the unfolding of the genetic program during the period of ontogenetic development.

The individual organism, therefore, has many of the characteristics of a dissipative structure: energy is actively acquired, time-delayed, and processed as it proceeds to a state of least dissipation. But notwithstanding these attributes, the individual organism lacks two vital characteristics of the dissipative structure: (1) continuity, and (2) the capacity for fluid adaptation to change. An organism has only the limited continuity of its individual life span (perhaps not strictly true for some lower organisms), and it can only adapt to environmental conditions within the range established by its genetic makeup at inception. It is only through a restructuring of the genetic makeup by the processes involved in mutation, recombination, and selection that adaptation to a different range of variables can be achieved. It is only within the continuum of the ecodeme, a group of like individuals, interacting within the constraints of the niche boundaries, that a fully functional dissipative structure develops.

The Basic Hypothesis

If an ecodeme within an ecosystem functions as a dissipative structure, then it is possible to make the following statements:

1) Each ecodeme will be dependent on a specific energy fluctuation; it will constantly tend to increase its energy acquisition from this fluctuation under the prevailing environmental conditions, and to conserve, to the greatest extent possible, the energy so acquired. The state of an ecodeme will depend on its individual capacity to integrate energy acquisition and conservation.

2) A dissipative structure will tend to proceed towards equilibrium, but by definition this can never be attained; it will therefore tend to assume a unique state of least entropy production as close as possible to its imaginary equilibrium.

3) For the ecodeme as a whole to reach a state of least entropy production, it must function as an organized, coherent group and not as a mere collection of individuals. Organization and coherence is achieved through *equal* interaction of individuals within the niche boundaries.

4) An organized group will display order (uniformity) and a common goal (the unique state of least entropy production).

The following statements can be made about the ecosystem as a group of interacting ecodemes:

1) As each ecodeme is dependent on a specific energy fluctuation, the configuration of the ecosystem will be determined by the component fluctuations within the total energy ambience. The energy ambience will be a function of the total solar energy and the pattern of its incidence combined with the sequence of changes in temperature, moisture, and nutrients as they occur at any particular site.

2) Within the ecosystem ecodemes interact *unequally*; this ensures that the system, as a whole, tends to proceed to a state of greatest energy flow and greatest entropy.

3) The tendency of each ecodeme to approach a state of least entropy production is counteracted by the system as a whole tending to a state of greatest entropy production. For an ecosystem to exist, the rate at which energy is assimilated must exceed or be equal to the rate at which it is dissipated.

4) An ecosystem may be said to be autonomous when it approaches the closed condition; a completely autonomous system will be one where all energy entering the system, whether as assimilated sunlight or as elaborated biomatter, is processed and ultimately dissipated as heat within the system boundaries. The flow of energy capable of doing work is therefore unidirectional.

5) Where the energy ambience exhibits a regular seasonal pattern, an autonomous ecosystem will reach a state of least oscillation, or steadiest state attainable in the prevailing environmental conditions. The steady state is the climax; at the climax energy acquisition and dissipation are equal.

6) To attain this state of least oscillation, the system, as a whole, functions as a series of coupled shock absorbers; organisms unable to achieve continuity will fluctuate, but fluctuation at each successive trophic level will be reduced until a state of least oscillation is reached.

7) A heterotrophic species generally will tend to induce increased energy flow and increased fluctuation in the species on which it feeds.

8) As species interact unequally, one species, the domi-

nant, is the one best able to integrate energy acquisition and accumulation, and is the one that oscillates least within the system. As a result the dominant is the species closest to its equilibrium and the one in which the characteristics of the dissipative structure are most clearly recognizable.

The Ecodeme as a Dissipative Structure

The first need is to establish the correspondence between the characteristics of an ecodeme and those of a dissipative structure. These characteristics will be most clearly recognized in the dominant species as being the one closest to its equilibrium position. That the dominant species in an autonomous ecosystem is proceeding to a state of least entropy production is manifest by the following characteristics: (1) a high degree of uniformity in size irrespective of age, (2) considerable size and age relative to other species in the system, (3) a long life span with high variances around the mean age of death to eliminate the tendency to oscillation that a fixed life span would cause, (4) potential recruits reduced to a level slightly greater than the number required for replacement, so that the greatest fraction of the energy available is devoted to biomass maintenance rather than energetically expensive growth, (5) a high degree of continuity indicating a continuous trend towards least entropy production and hence the existence of a damping moment. Together these characteristics ensure that maximum biomass is maintained, relative to the energy input, and that this biomass is kept in a state of least oscillation. Nonequilibrium is maintained by individual death and metabolic needs.

These characteristics exhibit also the existence of organization. Organization is most clearly shown by the *K*-configuration, where size uniformity or order is imposed on organisms irrespective of age, and the goal of least energy flow rate is achieved.

Other species in the ecosystem will tend towards equilibrium but they may be maintained in a state far from this position. Far from equilibrium their behavior may become quite specific, and even opposite to that indicated by the theorem of at least entropy production.

The capacity for an ecodeme to maintain coherence and organization can be attributed to three specific physical properties of the system: (1) regular fluctuations in the energy source, inducing the formation and maintenance of dissipative structures, (2) energy equipartitioning and homeostasis through uniform interaction between individiuals, as described by Soodak and Iberall (1978) under the doctrine of homeokinesis, and (3) the constraints provided by the niche boundaries.

Regular fluctuations in the energy ambience are produced by the rotation of the earth upon its own axis and by the annual seasonal changes brought about by the earth's rotation around the sun; these fluctuations are the basic source of order. Niche boundaries reduce dispersal of the organisms and necessitate interaction between individiuals; if the boundaries are impassable then the interaction between like individuals will tend to be uniform giving rise to energy equipartitioning and homeokinesis.

The concepts of homeokinesis are derived from the principles of statistical mechanics; like-atomisms interact in a manner such as to ensure energy equipartitioning, but in contrast to the variable energies of gas molecules in a closed container, the energy of the atomism tends to remain constant over a sequence of collisions. Soodak and Iberall define homeokinesis as:

"...the achievement of homeostasis by means of a dynamic regulation scheme whereby the mean states of internal variables are attained by the action of thermodynamic engines." ..."Such complex atomisms do not equipartition interaction energy per collisional cycle, but instead internally time-delay, process and transform collisional inputs using many fluid-like steps."

It is through homeokinesis that the interacting group of individuals is welded together into a functional dissipative structure. If the individual has the tendency to proceed to a state of least entropy production, then imposed uniformity will ensure that the interacting group will also proceed to a state of least entropy production.

The laws of thermodynamics demand that any interaction between systems or subsystems involving irreversible processes will result in an increase in entropy. Homeokinesis implies that work is done in the irreversible processes that are essential to its functioning, such as the gathering, storage, processing, and retrieval of the necessary knowledge of the encounters; each interaction will therefore result in a slight increase in the rate of entropy production. This enforced expenditure of energy runs counter to the individual goal of least entropy production. Encounters would therefore be avoided and dispersal take place if it were not for the presence of the niche boundaries. These enforced encounters give rise to a degree of mutual antipathy, which is, in turn, overridden by the superior authority of the trend to least entropy production, arising out of the essentially uniform interaction between individuials. In this way the individual loses a degree of autonomy; its goal is subverted to the goal of the group, but the group goal is merely that of the mean of all the individuals. This may best be described as a mediocrity trap imposed by peer pressure.

Out of this enforced trend to least entropy production on the part of the group arises cohesion between the individiuals. Cohesion within a group tending to least entropy production may be regarded as the counterpart of dispersal in the system tending towards increased entropy. The reality of cohesion can be deduced from the existence of autonomous individual organisms, that is, organisms that are free from immediate constraints governing form and activty in exactly the same way that, at a superior hierarchial level, herds, schools, flocks, or societies exist as autonomous groups free from the immediate constraints of their niche boundaries. That is, individual organisms and certain animal aggregations band together as organized units even in the absence of external constraints imposing common cause.

The field evidence to support the existence of an antagonistic-cohesive mechanism is very strong. The work of Breder (1954) on schooling in fishes, although criticized by Cushing and Harden Jones (1968) for being without apparent causative mechanism, provides one of the clearest examples of the existence of mutual antagonism existing under the overriding authority of a cohesive factor. Breder recognized that attraction between individuals is high when the distance between fish is large, but diminished with closer proximity; at a specific distance this attraction is balanced by a repulsive

force. This neutral point determines the spacing between individuals in a particular school, and the resulting cohesion allows the school to function as an organized unit. Within the niche it must be postulated that a certain number of these autonomous, independent groups fill the total space available. Similar evidence of cohesion in fish was obtained from Arctic charr stocks in Little Nauyuk and Gavia lakes during the experimental fishing program described above; in this case a high level of cohesion was maintained in the face of greatly reduced stock density (Johnson 1981).

A cohesive group of such a nature will be capable of functioning between the limits of total cohesion and total anarchy. If rigid uniformity is imposed on the group, then it will be condemned to function through innate behavior patterns as individuality is suppressed. Maintenance of more positive individuality, and at the same time allowing cohesion of the group will allow the development of 'leadership,' whereby individual experience can modify the behavior pattern and allow a more flexible approach to unusual situations. At the other limit total individuality results in anarchy and complete loss of cohesion, a state that is approached by animals defending individual territories, although even in such cases a considerable level of organization is maintained through the operation of equal and opposite interactions. It appears that these various patterns have developed in response to different patterns of energy availability — the autonomous group (school, herd, etc.) to a patchiness in the energy supply, division into territories, to uniformity in availability.

The antagonistic response of one individual to another results in intraspecific competition, but as it is between individuals that are essentially equal, it tends to be limited; that is, it is not pursued to the limit imposed by the death of one of the competitors, as this would be inconsistent with the group goal of least entropy production. Such generalizations are not universal, as the existence of cannibalism clearly indicates, but it is equally apparent that universal cannibalism would rapidly destroy the tendency to least entropy production, so that both internal and external to the ecodeme there would be a trend to increasing entropy production which would rapidly bring about the total collapse of the system.

The conclusions with respect to the imposition of uniformity on the individual through interactive processes is strongly reinforced by the work of Lerner (1954) and Falconer (1960), who showed that, with an interbreeding group, the individuals with greatest fitness are those having phenotypic characters closest in value to that of the group mean. Under these circumstances adaptive change will only occur through the accumulation of small unidirectional departures from the mean. This conservatism, within the constraints imposed by the characteristics of the nourishing energy fluctuation, results in a strong homeostatic mechanism.

By such small adaptive changes the ecodeme nestles within the generative energy fluctuation; likewise the ecodeme will adapt to small changes in that fluctuation. On the other hand abrupt change in energy availability may cause loss of homeostasis, so that individuals, formerly too aberrant, are now the ones most favored to survive. Phenotypic change in response to change in energy configuration may not occur immediately since the cohesion, built up under conditions of constraint, may continue in existence long after the constraints are removed.

Each ecodeme develops under the homeostatic control of a regular energy fluctuation that it has identified; each identifiable fluctuation must be able to transfer sufficient energy to the dependent ecodeme to ensure its existence from one input cycle to the next; in this context the ecodeme functions as a flywheel in its capacity to store energy. An increase in energy input, such as to magnify small irregularities that formerly contained insufficient energy to support a species, may result in fragmentation of the ecodeme or in its partial replacement by another species. At the other extreme an increase in energy input that narrows the base of the fluctuation relative to its height, resulting in greater intensity of input, will reduce the tendency to fragmentation and increase the biomass of the most favored species.

Perhaps one of the most conclusive pieces of evidence that the ecodeme functions as a dissipative structure might by itself be regarded as an anomaly. Certain organisms, such as some of the Pacific salmons, *Oncorhynchus* spp. and the periodical cicada, *Magicicada septendecim*, have fixed life spans; this is contrary to the goal of least entropy production since it will tend to stimulate oscillation. However, species with fixed life spans appear to depend on oscillation as an isolating mechanism. A species that benefits in this way from fluctuation in numerical strength, a situation into which it is initially forced by environmental conditions, will ultimately evolve characteristics to promote fluctuations. As Prigogine (1978) has observed, the behavior of a dissipative structure far from equilibrium may be quite specific and even opposite to that predicted by the theorem of least entropy production.

The Ecosystem

An ecosystem may be regarded as the point of overlap of a number of individual niches. The term was originally coined by Tansley (1935) to avoid usage of the expression 'biotic community' when referring to a group of plants and animals living together and interacting within the same precinct. Although his strictures have largely been ignored, community and ecosystem having become virtually interchangeable terms, there is no justification for the use of the term community in the present context. For the greater part, each ecodeme is seen as being in constant competition with all the remaining ecodemes, hence together there is a complete lack of communal purpose; it is, in fact, the individual ecodeme that represents a community and expresses a communal goal through mutual and uniform interaction.

Within an ecosystem the constituent species interact and because no two species are identical, interactional levels will be unequal. In the absence of modulating factors the interaction will proceed to the limits imposed by the inherent characteristics of the species involved. Only in the special cases resulting in commensalism or symbiosis can interspecific interaction be regarded as being limited and equal, and therefore of mutual advantage.

As all interactions of a nonreversible nature involve an increase in entropy, or in the nonequilibrium system an increase in the rate of entropy production, the essentially unlimited nature of the interactions between the ecodemes ensures that the system, as a whole, proceeds to the state of greatest entropy production attainable.

A second antagonistic process is now readily identifiable: the individual ecodeme proceeds to a state of least entropy

production, the system as a whole tends to proceed to the greatest attainable rate of entropy production. But, for an ecosystem to exist at all, the rate at which energy is assimilated (E_{ass}) must exceed or equal the rate at which it is dissipated (E_{diss}):

$$(3) \quad E_{ass} - E_{diss} \geq 0.$$

The system will thus tend to proceed towards a steady state in which energy assimilation and dissipation take place at equal rates.

This steady state, or climax, thus represents greatest accumulation of energy (or least rate of energy flow) that each ecodeme can achieve in the conditions prevailing; it also represents the greatest rate of energy flow that can be achieved by the interaction of the individual units. Each heterotrophic ecodeme may be regarded as tending to reduce, to a least value, the energy flow through its own substance, but to increase, to the greatest rate, the flow through the substance of all other ecodemes with which it interacts. Autotrophic ecodemes will arrogate to themselves the maximum energy attainable, to the detriment of autotrophs in the system.

The continual interplay between these opposing trends, under a variable energy input, will maintain a continuous 'streamlining' of the energy flow through the whole system. Streamlining of the energy flow will prevent excessive accumulation of energy in any region of the ecosystem and tend to reduce oscillation in abundance. This characteristic of natural systems has been recognized, at least since Herodotus in the 5th century B.C., under the general concept of the 'balance of nature' (Egerton 1973).

At the steady state a nonequilibrium system will exhibit a tendency for the energy to flow through the greatest number of pathways possible, as an equilibrium system tends to assume the greatest number of alternative states. The species in the nonequilibrium system will represent nodes on the network of possible pathways, hence within an ecosystem there will be a constant tendency for new pathways to develop either through fragmentation of existing species or the immigration of new ones. A system will therefore tend towards increasing diversity when diversity is defined inthe usual way (Hurlburt 1971; Orians 1975) as a function of the number of species present (species richness) and their individual abundances (species evenness or species equitability) — then high diversity is equivalent to high dispersal; high diversity implies a large number of species all uniformly represented, low diversity is few species with highly disparate representation. Leaving aside, for the moment, the question of different levels of entropy production caused by species of different complexity, the entropy of a system will thus be capable of being computed, on a relative basis, by the Maxwell–Boltzmann equation (Eq. 2). The similarity between this formulation and the frequently used diversity index derived from Shannon–Wiener (Shannon and Weaver 1949) information theory is apparent, but the origins are different. It is also important to recognize that when differences in entropy or entropy production are being compared, either within or between systems, the entropy must be computed on the basis of the total energy of the system. For a given energy input and a certain level of diversity, there will be a specific rate of entropy production; this will determine the total energy accumulation in the biomass. If the diversity increases while the energy input remains constant, then the rate of entropy production will increase and the accumulated energy decrease.

This tendency towards increased entropy production with increasing diversity can be most readily recognized when there is an increase in vertical dispersal. As energy passes along the food chain, each transformation necessitates a high expenditure of energy relative to that transformed; according to Brylinsky and Mann (1973), 10% of the energy passes from one level to the one above, with 90% being dissipated as heat during the work processes involved. An increase in the number of transformations thus necessitates an increase in the rate of energy flow through the system. The high level of energy expenditure at each transformation ensures that the trend to increased diversity is, effectively, self-limiting.

The excitation, that is, the total pattern of energy input both with respect to time and amount, will determine the configuration of an ecosystem; the excitation will in turn depend on the pattern of energy availability and the receptor species or primary producers present to take advantage of it. Each species present is dependent on the identification and isolation of a discrete energy fluctuation; as diversity tends to increase continually, systems developing in locations where the ambient energy is capable of being divided into a large number of relatively small fluctuations will have the potentiality to be diverse. High horizontal diversity among primary producers will have the potential to give rise to high vertical diversity only when the total energy input is high and provided that the energy flow is not truncated either by its rapid loss from the system or by periodic catastrophe such as fire, intense storm, or loss of oxygen. In those systems where the energy is not capable of being greatly subdivided, either because its input pattern is one of intense fluctuation or because total input is low, the potential for diversity will be low. The actual diversity at any location will be dependent on the species that have in fact assembled, and their individual characteristics. Diversity, as shown by MacArthur (1975), will also depend on the regularity of the energy ambience from cycle to cycle. The greater the annual variability in climate, the less will be the diversity, since individual fluctuations will lose their coherence and will be more difficult for a given species to identify.

The degree of autonomy of an ecosystem will determine the extent to which biomatter leaves the system, either by emigration or its removal by predators or grazers largely external to it. Loss of biomatter will tend to promote oscillation and prevent the system from reaching the steadiest state possible. Where biomatter is itself a primary source of energy, as in caves or the deep seas, the characteristics of its availability will determine the structure of the dependent systems in a way comparable with light energy entering a surface system.

The configuration of an ecosystem will thus be dependent on the following factors: (1) the characteristics of the energy ambience, (2) the length of time the ecosystem has been in existence and the rate at which species have assembled either by immigration or evolution, (3) the nature of the individual species arriving, and (4) the degree of atonomy of the system.

Each of these factors gives rise to specific and discernible characteristics that are readily identified in natural ecosystems. In view of the number of factors, and the wide range of values that each manifests, the specific situation is fre-

quently so complex that the major determinants are extremely difficult to assess. Certain systems, however, are dominated by specific constraints that allow general emergent properties to be recognized.

The ecosystem exhibiting the greatest diversity is the tropical rain forest, particuilarly that of South America; at the other end of the scale is the Arctic lake with its comparative simplicity. As Golley (1972) observed, the maintenance requirements in a tropical forest are extremely high, this implies a high rate of energy flow or a high rate of entropy production relative to the energy input; in spite of this high rate of energy flow, immense biomass is maintained as a result of the very high energy availability. In the Arctic lake low diversity combined with low annual temperature ensures long turnover time, and therefore biomass, relative to energy input, is high.

Within these polar positions a major geographical trend has been recognized for a long time; Wallace (1878) was the first to point to the existence of a trend in increasing species richness from the poles to the tropics; subsequently the causes of this gradient have come under considerable discussion (Fischer 1960; Connell and Orias 1964; Pianka 1966; Schall and Pianka 1968; Terborg 1973). Tramer (1967) has shown that species richness is correlated with diversity.

According to the present hypothesis, organisms are dependent on energy fluctuations; these fluctuations are primarily derived from the daily and seasonal changes brought about by the rotation of the earth on its own axis and the earth's annual rotation around the sun. Greatest diversity will develop where the energy available is most abundant, and where it is continually available at a high level throughout the seasonal cycle. This implies a warm, moist, tropical climate with little variation in energy availability both within and between years. Once a single organism is introduced into such an environment, the potential for fragmentation becomes immense and this will be further stimulated by irregularities in the substratum. As structure develops new microenvironments will be continually created and within each there will exist a new energy fluctuation available for exploitation by any organism capable of adapting to it.

It is thus in the regions now covered by wet tropical forest that the greatest diversity is to be found, and comparably in the aquatic sphere greatest diversity is found on the coral reefs of tropical waters. It is in these regions that energy is almost constantly available throughout the year; moisture, nutrients, and ambient temperature fluctuate little, and annual variability is very low.

Moving towards higher latitudes the overall environment becomes more heterogeneous as varition in daylength increases and seasonal fluctuations become more pronounced. Constraints are imposed on the extent to which the heterogeneity of the excitation can develop. Superimposed on this is the general reduction in total energy available as distance from the equator increases. The combined result of these factors is a general trend towards reduced diversity.

However, climate is not the only constraint on energy input so that in certain circumstances it is possible to observe specific effects in isolation. The effect of intensity of the input fluctuation is recognizable in the production of anchoveta, *Engraulis ringens,* in the Peruvian Current, off the coast of Peru. Although almost on the equator, an intense energy pulse is created by nutrient upwelling, resulting in a comparatively simple system that terminates in the massive production (10 million t annually) of a single species (Schaefer 1970). Simplicity in this system is maintained: (1) by its highly open nature so that the biomass is removed very rapidly by the local seabird population and (2) by long-term instabilities resulting from the intermittent failure of the upwelling.

A similar pulse of nutrients, frequently augmented by the wastes of industrial society, occurs during the spring and fall overturn of temperate lakes; this induces a massive bloom of relatively few, algal species (Hutchinson 1973; Vallentyne 1974).

The effect of the length of time a system has been in existence and the rate of species assembly can best be appreciated through consideration of isolated oceanic islands. When compared with their mainland counterparts, such islands show much lower diversity; as Mayr (1976) has suggested these islands have not reached 'faunal saturation.'

This may be explained by: (1) the comparatively short time that many oceanic islands have been in existence, (2) their isolation so that the rate of immigration is low, (3) their small size limiting potential mutation rate because of a comparatively small number of individuals of each species, and (4) their small size tending to limit the range of environmental conditions existing.

The low diversity ensures relatively low rates of energy flow that, in turn, give rise to energy accumulations capable of being reduced by the appropriate invader. The classical case, and one in which man cannot be implicated, is that of Darwin's finches in the Galapagos Islands (Lack 1947). Certain finches arrived from the mainland and became established, then subsequently adapted to the energy accumulations available, radiating into a large number of different niches as they responded to identifiable energy fluctuations.

In many other island ecosystems invaders have been assisted by man through the transportation of animals, intentionally and unintentionally, and by opening of access to new plant invaders by lumbering and agriculture. This has frequently led to disasterous effects on the island biota (Elton 1958); significantly it is the well-watered, isolated islands of midlatitudes (Hawaii, Mauritius, New Zealand, etc.) that have suffered most from invaders. Islands in high latitudes appear to have suffered little owing to the low total energy available and the high level of annual heterogeneity which, together, give rise to low potential for diversity. These restrictions are reinforced by the need for organisms to have some degree of preadaptation to the rigorous climates experienced (Saville 1972).

The inherent nature of the individual species present has a significant effect on the structure of an ecosystem; for example, Whittaker (1970) points out that eucalypt forest in parts of Australia develops under a climatic regime, that in other parts of the world would give rise to grasslands.

As is to be expected, it is the dominant species that are most significant in influencing structural characteristics. Dominance, in that it reduces energy flow to the greatest extent, will be most effective in reducing diversity. As Connell (1978) concludes, small continuous perturbations reducing dominance have the effect of increasing diversity. Dayton and Hessler (1972) also attribute the development of diversity in deep-sea faunas to continuous low-level disturbance reducing

dominance. Paine (1966) showed by direct experiment that the removal of a specialized predator on a species that could then assume dominance had at the same time the effect of reducing diversity. It has also frequently been observed that diversity increases during succession up to the penultimate stage but is reduced in the final stages as the full effect of the emergent dominant is experienced (Whittaker 1969).

New introductions, also, can have great effect on changing structural relationships. Zaret and Paine (1973) documented the introduction of certain fish species into Central American lakes that immediately assumed dominance. The new dominants rapidly brought about a great reduction in the diversity of the indigenous fauna. Similarly, Harper (1969) described how the removal of a relatively recent immigrant, the rabbit, *Oryctalagus cuniculus*, from English downlands, allowed a great increase in plant diversity. Martin (1967) has suggested that the arrival of man in continental North America occasioned the extinction of much of the Pleistocene megafauna. New introductions appear, as Slobodkin et al. (1967) suggest, to be particularly severe in reducing diversity. This reduction in diversity is, in all probability, only temporary on an evolutionary time scale, for as soon as conditions settle down, the inexorable march towards increased entropy production is resumed.

A closed system will proceed to a state of least oscillation, or maximum steadiness attainable, since it is only within the closed system that the full functioning of the shock absorber effect can be achieved. Removal of biomass either by external agents or through migration will result in faulty coupling of the shock absorbers and loss of effectiveness. The biosystem, or total integrated complex of the living world, existing within the biosphere, forms a completely closed system and therefore tends to a condition of maximum steadiness; the actual degree of steadiness achieved will depend on the nature of the excitation. Within the biosystem most of the component ecosystems are to some degree interconnected, but there is considerable variation in the extent to which, individually, they approach the closed condition. Perhaps it is only the systems existing under permanent ice in Antarctica (Goldman 1970) that achieve full autonomy; all others exhibit a greater or less degree of biomatter interchange.

Stability

A number of systems have been categorized as being stable: tropical rain forest (MacArthur 1955), deep-sea faunas (Sanders 1969; Slobodkin and Sanders 1969), cave faunas (Poulson 1963), and more recently Arctic lakes (Johnson 1976, 1980). On close examination all these systems approach a closed condition and therefore exhibit a high degree of steadiness. In wet tropical forests there is little migration, even in birds (MacArthur 1972), and virtually none in other classes. In caves and in the deep seas the flow of biomatter is unidirectional, with very little energy returning to the surface regions except in the form of heat. Arctic lakes, indeed all lakes of appreciable size and depth, particularly in their offshore regions, exhibit a low level of biomass interchange. All these systems have a high degree of autonomy.

It has been observed that ecosystems develop stability in the face of the environmental conditions to which they are subjected; as May (1975) states an ecosystem develops a robustness proportional to the harshness of the environment in which it is formed. Robustness therefore develops in response to the extent of the variations in environment regularly experienced over the course of the history of the ecosystem. Harshness of the environment is a compound function of low energy input and a high degree of variability within the year or overall environmental heterogeneity; it is, in fact, the opposite of favorableness (Terborgh 1973) which may be defined as overall environmental homogeneity combined with high energy input. The excitation of the system in harsh conditions thus tends to be homogeneous since external constraints prevent fragmentation of the available energy. Low total energy allows few species because each species present must obtain sufficient energy to maintain the flywheel effect and continue in existence. Homogeneous excitation is thus the equivalent of low diversity. Heterogeneous excitation develops in favorable environments where there are few constraints on the maintenance of homogeneity. Homogeneous excitation develops in environments having one or more of the following characteristics: (1) low energy input resulting from low temperatures or high winds, (2) physiological restrictiveness, as in salt marshes, (3) a high degree of variability within each season, as on mountain tops or on the Arctic tundra, (4) year-to-year variability as in deserts and to a degree in many grassland or prairie regions, and (5) nutrients limiting except for short periods in the year, as in aquatic upwelling or turnover situations.

All systems with homogeneous excitation will be, to an extent, stable, since the energy pathways within them will be short and direct; but for greatest stability the system must also show a high degree of autonomy and a high total energy input so that flow rates are rapid and system repair is executed expeditiously.

In this context Hurd et al. (1971) have provided a most satisfactory definition of stability, based on thermodynamic principles. Stability is the capacity to return to the ground state following perturbation by an external agent; the *degree* of stability is characterized by: (1) the amplitude of the deflection from the ground state, (2) the rapidity of the response, and (3) the rate at which the deflection is damped. Steadiness therefore implies sufficient stability to overcome the perturbations normally experienced.

An external perturbation is one that does not change the driving variables or parameters, that is, where there is no change in the energy ambience or the species richness, although diversity may be changed considerably; it is merely state variables that are altered (Holling 1973). Internal perturbation involves a change in the driving variables or parameters.

The most stable system that can be devised, in the face of a simple external perturbation, such as the removal of biomass, will be an autonomous one where the specific energy input is homogeneous and large in total amount. This implies a short, intense, energy pulse of large energy content, giving rise to an ecosystem of few species but high biomass. Simplicity can be maintained by building a small, specified amount of annual variability into the timing of the pulse; this will function as an isolating mechanism. The autonomy of the system will allow the accumulation of biomass and the build-up of a significant damping moment.

The amplitude to which a system of this type can be

displaced will be dependent on the biomass that can be removed without distortion of the recovery process. This will be dependent on the simplicity of the system and the total energy accumulated. The response time will also be governed by the level of input and the simplicity; short direct energy pathways and high rates of flow will ensure rapid return to the ground state. Damping will be dependent on biomass accumulation and this will be most significant at the level of the dominant; biomass accumulation will be dependent on slow turnover times, hence the factors favoring biomass accumulation will be contrary to those reducing response time. To achieve maximum stability it is therefore necessary to compromise between rapid turnover giving rapid response time and slow turnover giving a high level of damping. The degree of damping necessary will be dependent on the variability of input. A very simple system with a very regular annual energy input will be capable of being perturbed annually without oscillation being induced; as the annual variability increases, so oscillation will increase and the need for damping become more apparent. The shorter the response time the more the system will reflect changes in energy input.

One of the most stable systems known is that described by Coulter (1963, 1970, 1976) existing in the offshore waters of Lake Tanganyika. An upwelling of nutrient-rich water, combined with the very extensive and comparatively homogeneous nature of the offshore environment, has stimulated a relatively simple system with comparatively short food chains. In the higher levels of the food chain there are two, essentially annual, species of clupeid fish, *Limnothrissa miodon* and *Stolothrissa tanganicae*, which support three species of *Lates* and one of *Luciolates*, as the terminal fish predators. Prior to exploitation each of the four top predators showed a very pronounced *K*-configuration for its length distribution, indicating considerable damping capacity. Although tropical fish are difficult to age, Coulter estimated the turnover time of one of the *Lates* species to be between 5 and 7 yr. There appears to be a satisfactory compromise here between turnover and accumulation. This comparatively simple system in the offshore waters may be contrasted with the littoral region of the lake where at least 193 species have been identified (Lowe–McConnell 1975).

The open-water system of Lake Tanganyika appears to have all the attributes of high stability, a situation recognized by Coulter intuitively. These are (1) high biomass to support a high deflection, (2) relatively short turnover time and high energy input to ensure rapid response, and (3) accumulation of high biomass in the terminal stages to provide effective damping of variations in energy input. This system has, in fact, displayed considerable stability under heavy exploitation.

The Lake Tanganyika ecosystem has a number of similarities with that of an Arctic lake. Both are of relatively simple structure; in both, the dominant species has a highly developed *K*-configuration. However, in the Arctic lake energy input is very low so that processes are slow and therefore response time is long; but apart from long response time the Arctic lake must be considered highly stable in that it has a great capacity to withstand deflection combined with a very strong damping capability.

These relatively ponderous, autonomous systems may be contrasted with a highly volatile one such as that responsible for the immense production of anchovies in the Peruvian Current. Simplicity in this latter case is again initiated by an upwelling of nutrient-rich water allowing an intense energy input; it is maintained by the rapid removal of the energy by fishing birds and further augmented by great variability in energy input; at irregular intervals of a number of years there is almost total failure of the upwelling, with disastrous results to the bird population and more recently, the fishermen (Schaefer 1970). This system appears highly stable in the short term in its capacity to respond to perturbation; but this lasts only as long as the energy input remains constant. Paradoxically, this short-term capacity to respond rapidly is due to the simplicity maintained in part by the occasional failure of the input pulse over long time periods.

The salient features that gave rise to the diversity–stability hypothesis are now readily apparent. The wet tropical forest achieves a high degree of steadiness in the unperturbed state as a result of its autonomous character, but exhibits little stability with respect to external perturbations. Diversity ensures a high rate of energy flow through the system as a whole, giving rise to a constant tension in the energy pathways: a constant energy "hunger" that creates a dynamic damping moment. This dynamic damping will be more effective in damping large oscillations than small ones, as a stretched elastic cord rapidly eliminates large deflections, but is less effective in eliminating small ones. Provided the perturbation is not too severe, energy content will recover quite rapidly giving the same general form to the system, but the detailed readjustment may take a very long time. Richards (1964) quoting Chevalier (1948) reported that tropical forest at Angor Wat in Cambodia, had not regained the identical structure of the undisturbed forest 500 yr after original perturbation.

At the other end of the diversity–stability gradient, the small mammal members of the terrestrial Arctic ecosystem oscillate because they exist in relatively open systems subject to a high degree of annual variability. However, despite the openness of the Arctic terrestrial systems it must be mentioned that the largest terrestrial Arctic mammal, the musk-ox, *Ovibos moschatus*, has shown a remarkably high degree of stability in its recovery from near extinction in 1917 (when all hunting was banned) to the comparatively high levels of abundance it shows today (Tener 1965; Banfield 1974).

Little of generality can be said of internal perturbations as they may result from an immense range of possible changes in the driving variables and parameters. However, it is apparent that any change that increases the intensity of a fluctuation will tend to reduce diversity; most changes are likely to be of this type. From cultural eutrophication to agriculture, the end point is increased energy input to certain species and increased intensity of specific fluctuations resulting in reduced diversity and increased biomass. Occasionally perturbations may allow greater diversity to develop, but these will be mainly of the type that reduce the dominance of a particular species without disrupting the system in any other way. Increased diversity may be encouraged through increasing physical heterogeneity by, for example, provision of artificial reefs in shallow seas or increased planting of trees in cities and gardens.

An external perturbation only remains external provided that the interval between occurrences is greater than the length

of time required for complete recovery of the system. Repeated with sufficient frequency an otherwise external perturbation assumes the characteristics of an internal perturbation. Continuous distortion will create new internal energy values to which the system will adapt either by evolution or by the immigration of new species.

Finally there are two factors affecting the stability of a system that are inherited characteristics of the individual species: resilience and cohesion. Resilience is the capacity of a species to adjust its turnover rate to the current energy configuration, a capacity to increase growth and reproductive rate when losses to the ecodeme increase through increased predation or other form of exploitation. Individual species may vary very greatly in this capacity. Cohesion is the capacity to retain stock structure in the face of perturbation, as shown in the case of the Arctic charr (Johnson 1981); it is the attribute of animal aggregations to stick together in the face of disruptive events, the capacity to concentrate force in the face of an increasingly hostile world. Little, perhaps, is known about the operational mechanisms involved, but both features are undoubtedly of great importance in assessing the resistance of a system to disruption.

Energy Transfer

Thermodynamic theory postulates that one system (A) will capture energy from another system (B) if the entropy (S) relative to the total energy (E) of system A is greater than the corresponding value for system B:

$$(4)\quad \left[\frac{\partial S_A}{\partial E_A}\right]_{n.\beta} > \left[\frac{\partial S_B}{\partial E_B}\right]_{n.\beta'}$$

where ∂ represents a small change in the property it precedes and n and β are the number of particles and constraints, respectively (Keenan et al. 1974).

In very general terms this implies that a system with high entropy relative to its total energy will tend to capture energy from a system with low entropy relative to total energy.

In thermodynamic terms the temperature (T) regulates the flow of energy from one system to another; temperature is defined as the reciprocal of the capturing tendency and it is usually measured on the arbitrarily assigned Kelvin scale (°K).

$$(5)\quad T \equiv \left[\frac{\partial E}{\partial S}\right]_{n.\beta'}$$

When ecosystems interact energy will tend to flow from the 'hot' ecosystem where biomass is high, relative to the rate of entropy production to 'cold' systems where biomass is low, relative to entropy production; that is, from high latitudes towards the tropics, from regions where input fluctuations are high and homogeneous to regions where input is heterogeneous.

Within the individual ecosystem the energy tends to flow in the opposite direction; it flows from the highly fluctuating organism where turnover time is short to the dominant species where continuity is greatest. A large number of relatively small rapid fluctuations may be regarded as equivalent to high entropy, a comparatively small number of fluctuations having a long time period is equivalent to low entropy.

These two trends counteract each other and tend to come into a state of balance, although full stability is never achieved as there is always a tendency for the rate of entropy production to increase: entropy always "wins." The overall result is a slow drift of energy from high latitudes towards the tropics. This process is most readily seen in the annual migration of birds to high latitudes in summer for the period during which they incubate and rear their young; the net result is that more birds leave the rearing areas in the fall than arrive there in the spring.

These features of ecosystem structure make possible a number of generalizations:

1) The biosystem, as it forms a completely closed system, will tend to a state of maximum steadiness; all migration can therefore be regarded as patterns in the energy flow that tend to reduce locally recurring instabilities.

2) Tropical rain forest, having the highest diversity and therefore highest rate of entropy production relative to its energy input will have the greatest capturing tendency of all terrestrial ecosystems. Organisms entering such regions may become established if they can effectively increase the rate of energy flow or establish dominance, otherwise they serve merely as an additional source of energy. The energy flow capable of doing work therefore tends to be unidirectional, ensuring that the system has a high degree of autonomy. As this state of high entropy production remains relatively constant throughout the year there is little tendency for migration patterns to become established, and little tendency for species evolving in the tropics to move outside.

3) Dominance in ecosystems will develop in the first species along the food chain that is best able to integrate energy acquisition and conservation. First opportunity will accrue to the primary producers. In terrestrial environments where conditions are equable, where moisture relationships and temperatures provide a long growing season, dominance develops in the primary producers giving rise to forest cover (Whittaker 1970).

4) Where conditions are more erratic, too cool or too dry for forest cover to develop, grasslands or tundra become established. Under these circumstances continuity by the primary producers cannot be maintained, so dominance passes to the next trophic level: the primary grazing animal. On most of the world's grasslands, ungulates as the prime grazers have assumed dominance, but in areas of the world where mammals have made little significant penetration, the most suitable species to hand have assumed the role. In New Zealand, giant grazing birds, the moas *Dinornis* sp. and *Euryapteryx* sp. (Thompson 1964), were dominant before man's arrival in the mid-14th century; in Australia large grey kangaroos of the species *Macropus* fulfill a similar function.

5) In aquatic systems grazing and turbulence preclude the establishment of the primary producers as dominants except in very restricted environments. In hypersaline lagoons in Australia, stromatolites, climax associations of algae and bacteria, may develop and, in certain environmental conditions in the sea, kelp beds may occur, but in all other acquatic systems the primary producers undergo considerable oscillation. From the highly oscillating algae energy passes through a number of different trophic levels until dominance and continuity are

reached in the terminal stages of the food chain, either in the form of fishes or marine mammals.

6) Prolonged energy input may result in high diversity in primary producers, but if total input is low, or the energy flow truncated in other ways, the upper levels of the food chain tend to be short and of low diversity; this situation is characteristic of oligotrophic lakes. A truncation of seral development appears to give rise to the most diverse land flora in North America north of the Mexican border. This has developed in the Santa Catalina Mountains of Arizona (Whittaker and Niering 1965) where moisture relationships are inadequate to support full forest cover; greatest diversity exists between the forest at higher altitudes and desert conditions lower down. In the intermediate region there are two periods of rainfall annually which, in the warm conditions prevailing throughout much of the year, allow two growing seasons. This pattern of prolonged but low total energy input gives rise to an open woody–shrub formation that exercises a low level of dominance, but allows great diversity in the ground flora.

Fitness and Selection

Fitness is usually measured by the contribution to succeeding generations made by a single breeding pair. However, it is undeniable that reproduction, in itself, will tend to reduce fitness; the apparently excessive energy drain on many organisms is in itself detrimental to the maintenance of existence and opposite to the goal of least entropy production. It is difficult to understand how a character with such negative survival value has, in fact, survived unless additional factors are involved. Insofar as survival has, manifestly, occurred and species not only exist but tend to expand to the limits imposed by external constraints, reproduction and expansion are generally accepted as the "givens" of the life process and largely beyond further investigation or enquiry.

It is only when the interacting group of like individuals, within its niche, is regarded as a dissipative unit tending towards least entropy production, that the internal logic becomes apparent. Sexual reproduction takes place to maintain the coherence and continuity of the group, and, in fact, brings little benefit to the individual. As recognized by Fisher (1958) sexual reproduction is likely to have resulted from selection favoring the species rather than the individual. It seems quite clear that, as is evident in the higher vertebrates, a mating pair must be "bribed" by the prospect of pleasure to reproduce. The negative effect of reproduction on survival has to be offset by the drive to initiate the reproductive process.

A limited life span for each individual in the dissipative structure fulfills two functions and at the same time necessitates the reproductive process. Death combined with metabolic needs maintain the nonequilibrium state of the structure; death and replacement allow fluid adaptation to the energy ambience, and adaptation to new or changing environments.

This view of the role of the interacting group necessitates a complete review of its influence on the selective process. As described above, selection will be modulated to meet group goals where the group goal is the mean of the individual goals. A mechanism of this type exerts a strongly conservative or homeostatic influence on change within the group. Small advantages will be widely disseminated within the group and transmitted to future generations; large differences will not be tolerated.

Wynne-Edwards (1962) concluded that group selection is of great importance in many animal groups, but in general his ideas have not received wide acceptance because a mechanism appeared to be lacking. The recognition of the group as a dissipative structure establishes its preeminence in the selective process; under such circumstances it is by no means impossible to understand how characteristics with negative individual survival value, such as altruism, can be of great benefit to the group. A gene for altruism will not be eliminated from the general gene pool as it would be from the genetic makeup of an individual under individual selection.

On the other hand it seems unnecessary to postulate, as Wynne-Edwards does, that many social activities among animals are directed towards population "assessment" and adjustment of reproductive rate to control density. The mere existence of organization (a time delay in energy flow and the goal of least entropy production) will bring the dissipative structure to a state of least fluctuation, provided the energy availability fluctuates around a mean value.

It is undeniable that many social activities appear to foster group ends rather than those of the individual; these group activities may be regarded as an expression of cohesion serving to strengthen the basic organization.

Evolution

Simpson (1970) has argued that over the long period of time open to investigation, geological events have remained essentially constant in their intensity, in spite of a small overall decline in the energy of the sun–moon–earth system. This is in marked contrast with biological events where these same constant forces appear to have given rise to a great increase in diversity and complexity.

Although evolution has been multidirectional in general, Simpson (1969, 1970) recognizes three main trends: (1) a 6-fold, possibly 10-fold, increase in the number of species in existence today compared with the Cambrian period, (2) an increase in the distinction between types of organism in structure, function, and ecology, and (3) an increase in the structural complexity of some evolutionary lines and and increase in the average complexity of all. These major changes appear to have operated continuously over evolutionary time, even if neither smoothly nor always in the same direction.

A trend towards increased size is one of the most frequently observed features of evolution within a taxonomic sequence; this phenomenon has long been recognized as Cope's rule (Cope 1887, 1896). A particular taxon usually starts with small members which gradually evolve *towards* increased size (Stanley 1973a). However, in spite of this general trend, small size is, of itself, by no means a primitive trait (Mayr 1976).

The trend towards increasing diversity results from the fundamental trend to increased energy dispersal and the associated increase in the rate of entropy production. This trend will continue until an asymptote is reached, the position of the asymptote being determined by the energy ambience and the species assemblage. In reality the asymptote is unlikely to be smooth as new dominants will arise and temporarily reduce diversity, or climatic changes alter the energy configuration.

Increase in the distinction between types of organism is the result of increased dispersal within the framework of an essentially constant energy source. Evolution may be regarded as taking place in a cone-shaped hyperspace, time being represented along the main axis, with zero time as the apex. At any moment in time the existing species may be represented as those occupying on the base. The constant tendency to increased dispersal causes the base to expand. This expansion ensures that the energy available to each discrete group of like organisms becomes attenuated, since with increased dispersal comes greater diversity and reduced biomass relative to the total input; as the input remains constant, the share to each species will, on the average, be less. Because of this, as new species appear, the less efficient or the less effective in the prevailing conditions must disappear. In this way the links between survivors become more and more tenuous and in time disappear altogether. The remaining species in their turn tend to disperse and lose their connections with groups to which they were once closely related.

The general tendency towards increased complexity of individuals again arises from the attenuation of the energy pathways. With attenuation, energy becomes more difficult to acquire so that selection will be for structures facilitating acquisition; acquisition will be improved by better sensory mechanisms and improved locomotion. In the early stages of vertebrate evolution the alternative route was frequently adopted: that towards improving conservation by the evolution of heavy protective armor. This route is probably satisfactory when energy is relatively abundant, but in times of scarcity the heavily armored organism is at a disadvantage compared with the one that is more mobile. Mobility serves the double function of getting to the energy first and avoiding being caught doing so.

There is, however, a price to be paid for increased individual complexity in energetic costs. Increased complexity and increased activity necessitate an increase in energy flow rate; this is contrary to the trend to least entropy production. To stay in the game it is therefore necessary to give a little ground and increase the energy flow rate, but only just enough to meet the immediate need and maintain a satisfactory solution to the energy acquisition–conservation integral.

The greatest increases in complexity have evolved within the central arena of the biosystem, where the major energy resources are competed for. In this arena complexity has evolved to allow organisms greater freedom from environmental constraint, this represents a broadening of the base of their energy fluctuation in opposition to the trend towards increased diversity. Such increased complexity without restrictive specialization may be regarded as progress. In the first place there was the emergence onto land and then gaining freedom from a watery medium; this led to improved homeostasis and homeothermy; finally there was the capacity to think logically about overcoming environmental constraints. On the periphery of this arena, as each succeeding level of complexity has evolved, certain organisms have turned to a less competitive existence and assumed a specialized way of life. The absence of competition in a specialized niche allows an organism to obtain energy at reduced cost so that it forces itself ever tighter into the crevice of its specialization.

Increased size is one of the most effective ways of increasing the capacity to acquire energy and at the same time improve conservation. Not only does increased size improve the capacity to obtain nourishment through greater strength or greater height in plants, it also tends to reduce metabolic rate and provide escape from former enemies. The ultimate, if it can be attained, is the state of dominance and relative freedom from either grazers or predators.

The driving mechanism behind evolution can now be readily discerned. As diversity within an ecosystem increases and the energy flow rate increases, under constraint of a constant total energy supply, the energy available to each ecodeme will become attenuated. If one ecodeme responds to this situation by an improvement in its acquisitive capacity, it will further attenuate the supply to the remainder; this will, in turn, stimulate the remainder to increase their acquisitiveness. The energy flow through the system is thus self-accelerating, but the self-acceleration is strongly modulated by the governing necessity for each ecodeme to tend continuously to least entropy production.

The ecodeme, as it strives to maintain maximum time delay in energy flow, is thus beset by two counter trends: (1) the unequal interaction between all ecodemes tending to increase flow rates through the system and (2) the need to improve energy acquisition by increased complexity and increased activity, both necessitating an increased rate of energy expenditure. The rate of energy flow through the ecodeme therefore gradually increases with time as the acquisitive capacity keeps pace with the need for continued existence.

In the short term these trends promote a considerable degree of stability. This is achieved as in the manner of the triangle of forces in a mechanical system (Fig. 3).

Within these conditions natural selection can be seen as the continual testing of yesterday's satisfactory solution to the energy acquisition–conservation integral along with minor variants in the slightly faster moving world of today. The main prizes are not for the most expedient solutions, the road to expediency is the road to specialization; the main prizes go to the species that can widen their ranges of environmental tolerance, increase food supply, and generally broaden the base of the energy fluctuation upon which they are dependent. This capacity, on the part of the individual ecodeme, to increase and consolidate its energy base is offset by the continuous trend to increased heterogeneity on the part of the whole ecosystem.

Occasionally the trend to increased complexity is put into reverse when an organism enters a new environment and, surviving there, finds itself in possession of structures no longer serviceable. The classic case is that of organisms with eyes entering the total darkness of a cave environment; the eyes, now functionless and incapable of being turned to other uses, tend to be eliminated (Barr 1968). It seems, as Regal (1977) suggests, that this complexity is now merely noise in the system. The trend to least entropy production demands their elimination, but the slowness with which they are eliminated is a measure of the immense cohesion within the individual genetic line; characters that have evolved over long periods of time are not readily relinquished.

The earliest beginnings of life on earth must apparently be sought in a regular energy fluctuation imposed on a suitable chemical broth. A highly random energy impulse, such as the frequently postulated lightning flash, may perhaps have played a part in the development of suitable chemicals, but it

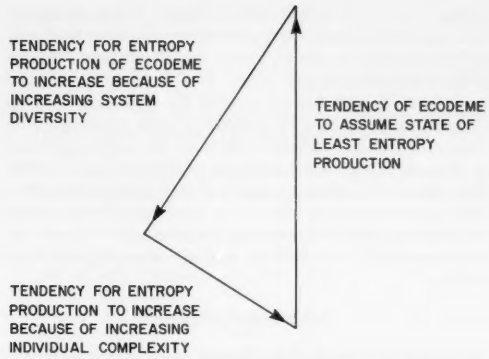
TENDENCY FOR ENTROPY PRODUCTION OF ECODEME TO INCREASE BECAUSE OF INCREASING SYSTEM DIVERSITY
TENDENCY OF ECODEME TO ASSUME STATE OF LEAST ENTROPY PRODUCTION
TENDENCY FOR ENTROPY PRODUCTION TO INCREASE BECAUSE OF INCREASING INDIVIDUAL COMPLEXITY

FIG. 3. The triangle of trends analogous to the triangle of forces in a mechanical system that creates temporary stability within an ecodeme functioning within an ecosystem. The tendency within the ecodeme to least entropy production is in opposition to the trends to increased entropy production through increased complexity and increased diversity. In general, over evolutionary time the triangle moves gradually towards a state of increased entropy production.

seems fairly conclusive that the origin of organized, as opposed to merely ordered, structures arose under the impact of a regular energy fluctuation. Before organisms could become established an element of time had to be incorporated within the fundamental chemical building blocks.

If this was the most important event in the evolution of our present day ecosystems the second was undoubtedly the event that led to the origin of heterotrophy in the Cambrian era (Stanley 1973b, 1974). The heterotroph may be regarded as an organism that evolved in response to increased energy dispersal and in doing so placed a new dimension on diversity. Heterotrophy is a Machiavellian device that allows one organism to live on the work of another simply by speeding up the rate of energy flow.

Once the grazing animal came into existence it would have rapidly eliminated the climax assemblages of algae and bacteria so prevalent in the Precambrian; grazing would have allowed diversity to increase within the algae by its elimination as the dominant; this in turn would stimulate increased algal fluctuation, more rapid energy flow, and an increase in primary production. From this position the evolution of a predator from a grazing animal would have been but a small step along the heterotrophic road.

The immense algal reservoir of the Precambrian, once broached, would have given rise to a tremendous energy cascade. In the unfettered conditions of such a cascade, diversification would have been rapid and largely dependent on whatever chance mutations came to hand. A steady state would have been reached relatively soon after the first explosive evolutionary outburst; once reached, the basic clay for evolutionary development over the next 500–600 million years was established.

Evolution can now be regarded as occurring in two different time frames. In the first there is the slow adaptation of a species to closer correspondence with the energy configuration on which it is dependent and at the same time a tendency to broaden the base of support by improving acquisition. In this way it is also possible to adapt to slow changes in the energy ambience. The second way is much more rapid and is occasioned by (or creates) a significant shift in energy values, leading to the emergence of the 'hopeful monster' (Goldschmitt 1940; Gould 1977). Long periods of Darwinian gradualism may thus be interspersed with brief periods of comparatively rapid change, revealed only by discontinuities in the geological record (Gould and Eldredge 1977; Stanley 1979).

Conclusion

The foregoing analysis of the emergent properties of ecosystems, for all its apparent complexity, is undoubtedly an oversimplification. By way of example two instances may be given. Over the course of development of an individual there is considerable increase in its complexity, which implies an increase in the rate of energy expenditure. Such a trend runs counter to, and is also masked by, the observable trend towards least entropy production shown by the overall reduction in metabolic rate over the same developmental period.

The second example is more readily subject to testing. Woodwell (1967, 1970; Woodwell and Whittaker 1968) has pointed out that the ratio of photosynthetic to nonphotosynthetic tissue increases with the severity of environmental conditions, whether these occur over a gradient of increasing latitude, altitude, moisture reduction or increasing levels of radiation. As photosynthetic tissue is more active metabolically than woody tissue, it may be regarded as having a higher rate of entropy production. This will give rise to a trend toward increased entropy production running from the equator to the poles. This again will run counter to, and be largely masked by, the dominating trend towards reduced rates of entropy production resulting from an intensification of environmental fluctuations.

This trend towards increased rates of entropy production with increasing environmental harshness seems to be identical with the trend isolated by Connell and Orias (1964) as a major factor in the reduction in species diversity with latitude. While not regarded as the major determinant in the present thesis it undoubtedly makes an important contribution to the total situation.

The ramifications of the concepts presented are far reaching and, if accepted, are likely to affect our attitudes in many fields, from resource management through sociology even to economic theory and philosophy. The first challenge seems to be the need to build new models to test the conclusions reached and then test them in real situations; not with the immediate aim of obtaining numerical solutions but to gain insight into the functional mechanisms existing.

If the human dilemma is to be improved it will be essential to allow organization to develop under the benign influence of a stabilized energy input; only in this manner can an oscillating population be brought under control.

Progress has been isolated as the trend towards a broadening of the environmental conditions in which a species can exist, while at the same time maintaining a state of nonspecialization. Man, through his ability to develop life-support systems in many fields, would appear to have reached the pinnacle of progress. This is not so; apart from the fact that much of the so-called progress is complexity for the sake of

complexity and involves a high degree of specialization, man has yet the hardest row to hoe if he is to achieve real progress: he must learn to live continuously in an environment of his own making and learn how to make his own environment worth living in.

To this end it is essential that a proper philosophy, dealing with these real biological problems, be developed, and, as we cannot avoid the mediocrity trap, such a philosophy must become part of the view of the average man or woman. As a start it seems necessary to return to Aristotle and pick up the threads of his teachings, for one of his central themes is also central to the present thesis. This is the search for causes, for it is only when we understand causes do we have scientific knowledge. According to Aristotle one of the causes of change is the existence of a 'telos' or goal, a perfect state towards which all things are proceeding.

Bertrand Russell (1946) has castigated Aristotle for introducing this concept into philosophy, a concept Russell believes to be a perversion. The element of distortion in incipient form was perhaps present in Aristotle's philosophy, his views on the divinity of the final cause are not always clear, but it was certainly theologians of the Middle Ages who magnified this aspect so that the teleological process came to be regarded as the unfolding of a divine plan for the perfection of the universe, particularly the perfection of man himself. The more scientific aspect of Aristotle's views on the physical nature of causes was eliminated. These views became anathema to many biologists following Charles Darwin's elucidation of the evolutionary process involving as it does many chance elements; chance could not be reconciled with the achievement of a specific goal.

Undoubtedly much of what Aristotle had in mind when developing his concept of teleology concerned the ontogenetic development of an individual organism from fertilized ovum to mature individual, an end-directed process that results in an imago or reproduction of a preceding form. This aspect can be set aside under the term 'teleonomy.' A teleonomic process or behavior is defined by Mayr (1976, p. 389) as one that owes its goal directedness to the operation of a program. In this way open or closed programs contained within the genome direct the development of the individual towards its goal as a mature organism, very similar to, but not quite identical with, many other individuals developed by comparable programs.

This, however, does not cover the more cosmic aspects of Aristotle's philosophy, the wider implication that all things are moving towards a telos or goal, so that present activity is, in fact, being influenced by a future state. If the telos is regarded as a thermodynamic state rather than a material or even nonmaterial identity, then a strong teleological process exists within the biosystem. The ultimate but unattainable goal of the ecodeme is equilibrium, the proximate goal is a state of least entropy production. The goal of the biosystem as a whole is the attainment of a steady state, but a steady state of a transient nature; over evolutionary time the goal is an ever-increasing rate of entropy production. These goals are approached through the interaction of the energy trends as they are modified by chance occurrences; this is a process of trial and success, with success being measured by the extent of the movement goalwards, which is natural selection.

These considerations give rise to a more general aspect, perhaps closer to Aristotle's original intent. Within the central arena where the major energy resources are competed for, it has been possible to identify a trend toward progress. Progress is the increasing mastery of all possible environments and man himself has advanced a considerable way along this path through maintenance of a generalized state combined with greatly increased complexity. However, to avoid complacency, it must be kept in the forefront of the mind that in terms of the Maxwell–Boltzmann equation this merely represents a trend to fewer pathways ($Pi \rightarrow 1$), a temporary victory over the long-term trend to increasing diversity ($Pi \rightarrow 0$) and one not uncommonly achieved by a newly emerging dominant species.

Acknowledgments

It is a pleasure to acknowledge the help and support of the following members of the staff of the Freshwater Institute: Dr Rudolf Wagemann, in particular, has shown a keen long-term interest, always ready for sympathetic discussion; Drs Togwell Jackson, Jim Clayton, Jan Barica, and before he left, Manfred Freese, all read earlier versions of the paper and provided many valuable comments. I also thank Dr Ramon Margalef of the University of Barcelona and Dr Harold Mundie of the Pacific Biological Station, Nanaimo, for their penetrating comments and stimulating criticism of a previous draft. I am very grateful to Dr E. G. Berry of the Classics Department, University of Manitoba, who helped me to reach a better appreciation of Aristotle and his contribution to biology and philosophy, and to Dr Herbert G. Baker of the University of California, Berkeley, who first opened my eyes to ecology and for later reading the manuscript and providing advice and encouragement. I thank Mr Roger Peet and the staff of the Fisheries Resources Section, Freshwater Institute, for their tolerance, understanding, and support, and for allowing the work to proceed in peace even in times of budget constraint. I particularly thank my wife, Cecile, who has borne the brunt of the vicissitudes of fortune over the years as the paper has struggled for maturity.

I am extremely grateful to Dr A. W. Mansfield, Director of the Arctic Biological Station, Ste. Anne de Bellevue, Department of Fisheries and Oceans, for allowing me to use data he collected in 1962 at Nelson Lake, Cornwallis Island, and also to Bruce Stewart and Gary MacDonald, for agreeing to resample Nelson Lake in 1980 and for allowing me to use the data.

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Recent Trends in Environmental Impact Assessment

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Printed in Canada (J6209)
Imprimé au Canada (J6209)

Abstract

ROSENBERG, D. M., AND V. H. RESH ET AL. 1981. Recent trends in environmental impact assessment. Can. J. Fish. Aquat. Sci. 38: 591–624.

The objectives of this paper are to characterize an "ideal" environmental impact assessment (e.i.a.); to review the contemporary status of e.i.a. for several major activities and areas of development; and to identify successes, failures, and future needs in e.i.a.

The institutional procedures to be followed for e.i.a. have been formalized in a number of countries, but the scientific basis and methods are still developing. We propose that the following elements comprise an ideal e.i.a.: (1) definition of scientific objectives, (2) background preparation, (3) identification of main impacts, (4) prediction of effects, (5) formulation of usable recommendations, (6) monitoring and assessment, (7) sufficient lead time, (8) public participation, (9) adequate funding, and (10) evidence that recommendations were used.

The "best available" predictive, preoperational e.i.a.'s involving aquatic resources (power plants, fossil fuels, recreation, reservoirs, wastewater treatment, forestry, and dredging and water diversion in estuaries) were reviewed and scored on a 0–5 scale for each of the elements identified above. Mean scores for the criteria which could be assessed (nos. 1–8) indicated that the quality of the best available e.i.a.'s does not exceed our defined average but improves when legally required documents are excluded from the calculations. The lowest means, for criteria within the scientist's control (nos. 1–5), were obtained for "Prediction of effects" and "Formulation of usable recommendations." Overall mean scores for each development area (criteria 1–5) indicated three broad groups which included studies of above average quality (wastewater treatment, recreation); studies of approximately average quality (estuarine impacts, power plants, reservoirs, and fossil fuels); and studies of below average quality (forestry practices).

Environmental impact assessment has had the following successes: increased environmental awareness due to public involvement in e.i.a., some environmental protection, and elucidation of intriguing research problems. The list of failures of e.i.a. is, however, longer: "tokenism," unrealistic time constraints, uncertainty of program or development schedules, difficult access to e.i.a. literature, questionable ethics, lack of coordination among studies, and poor research design.

Future organizational/administrative needs of e.i.a. include improved access to e.i.a. literature, increased accountability for e.i.a.'s and their authors, improved public input into project decisions and designs, and improved organization and presentation of e.i.a. reports. Future scientific/research needs include development of methods to define and quantify relationships between biological, esthetic, and economic impacts; support for independent biological inventory programs; adequate time frames; improved design of research; inclusion of monitoring and assessment in every e.i.a.; study of cumulative impacts on a regional or national scale; and improved communication between scientists and planners.

Key words: environmental impact assessment, aquatic ecology, power plants, fossil fuels, recreation, reservoirs, wastewater treatment, forestry, dredging and water diversion (estuaries)

Résumé

ROSENBERG, D. M., AND V. H. RESH ET AL. 1981. Recent trends in environmental impact assessment. Can. J. Fish. Aquat. Sci. 38: 591–624.

Le présent article a pour objectif la charactérisation d'une évaluation "idéale" de l'impact environmental (e.i.a. = *environmental impact assessment*); l'examen de l'état actuel des e.i.a. de plusieurs activités et domaines de développement majeurs; et l'identification des succès et des échecs, ainsi que les besoins futurs en e.i.a.

Plusieurs pays ont formalisé les modes opératoires institutionnels des e.i.a., mais on travaille toujours à mettre au point une base et des méthodes scientifiques. Les éléments suivants devraient, à notre avis, constituer une e.i.a. idéale: (1) définition des objectifs scientifiques; (2) préparation du dossier; (3) identification des principaux impacts; (4) prédiction des effets; (5) formulation de recommandations utilisables; (6) contrôle et évaluation; (7) délai suffisant; (8) participation du public; (9) financement adéquat; et (10) indications que

les recommandations sont suivies.

Nous passons en revue les meilleures e.i.a. préopérationnelles et prévisionnelles disponibles concernant les ressources aquatiques (centrales électriques, carburants fossiles, récréation, réservoirs, traitement des eaux usées, exploitation forestière, dragage et déviation des eaux dans les estuaires). Nous les avons cotées sur une échelle de 0 à 5 en rapport avec chacun des éléments mentionnés ci-dessus. Le pointage moyen pour les critères évaluables (n^{os} 1−8) indique que la qualité des meilleures e.i.a. disponibles ne dépasse pas la moyenne que nous avons définie, mais s'améliore quand on exclut des calculs les documents requis par la loi. Dans le cas des critères pouvant être contrôlés par un scientifique (n^{os} 1−5), les moyennes les plus basses sont celles de "prédiction des effets" et "formulation de recommandations utilisables." Si l'on fait la moyenne générale dans chaque domaine de développement (critères 1−5) on obtient trois groupes: études de qualité supérieure à la moyenne (traitement des eaux usées, récréation); études de qualité à peu près moyenne (impacts sur les estuaires, centrales électriques, réservoirs et combustibles fossiles); et études de qualité inférieure à la moyenne (exploitation forestière).

L'évaluation de l'impact sur l'environnement à marqué des succès sur les points suivants: une meilleure conscience de l'environnement par suite de la participation du public aux e.i.a.; un certain degré de protection de l'environnement; et l'éclaircissement d'intrigants problèmes de recherche. Par contre, la liste des échecs des e.i.a. est plus longue: politique de coopération symbolique; limites de temps non réalistes; incertitudes quant aux programmes et à leur calendrier; difficultés d'accès aux rapports des e.i.a.; morale douteuse; manque de coordination entre les études; et mauvaise organisation de la recherche.

Parmi les besoins futurs, tant sous le rapport de l'organisation que de l'administration des e.i.a., on note: un meilleur accès aux publications des e.i.a.; une responsabilité accrue des e.i.a. et de leurs auteurs; une plus grande contribution du public aux décisions et à l'organisation des projets; et une meilleure organisation et présentation des rapports d'e.i.a. Parmi les besoins futurs en science et en recherche, on doit mentionner: mise au point de méthodes de définition et de quantification des relations entre les effets biologiques, esthètiques et économiques; appui à des programmes indépendants d'inventaires biologiques; délais adéquats; meilleure organisation de la recherche; inclusion d'un contrôle et d'une évaluation dans chaque e.i.a.; étude des répercussions cumulatives à échelle régionale ou nationale; et meilleure communication entre scientifiques et planificateurs.

Received August 29, 1980
Accepted February 5, 1981

Reçu le 29 août 1980
Accepté le 5 février 1981

Introduction

Objectives

The overall objective of this paper is to examine the use that research based on the scientific method can have in assessing environmental impacts. Emphasis has been placed on environmental impacts that involve aquatic ecosystems. The specific objectives are to characterize an "ideal" environmental impact assessment; to review the contemporary status of environmental impact assessment for several major types of developments, mainly in North America; and to identify successes, failures, and future needs in environmental impact assessment.

The success of an environmental impact assessment depends on a broad array of factors ranging from project management to dissemination of information to the public. However, we maintain that research based on the scientific method is a fundamental and necessary part of environmental impact assessment. Our main concern in this presentation is to explore ways to improve the research portion of this process. Although we expect that researchers in aquatic ecological disciplines will be the main audience, our treatment should be useful to researchers in other scientific disciplines involved in environmental impact assessment. Hopefully, the research approach will be of interest to specialists involved in other phases of environmental impact assessment as well (e.g. economists, regional planners, politicians, bureaucrats, social scientists, engineers, lawyers, etc.).

Increasing demand for environmental impact assessment has created a need in universities for graduate-level training in the assessment of environmental impact according to scientific principles (e.g. Plewes and Whitney 1977; Erickson 1979). Students should also be familiarized with the broad range of developments being assessed and the contemporary quality of these assessments. This paper is an outgrowth of such a course given during the 1979 winter quarter in the Department of Entomological Sciences, University of California, Berkeley, CA.

Definitions of Environmental Impact Assessment

We use the term "environmental impact assessment" (hereafter referred to as e.i.a.) to refer to an analytical process, as opposed to legally, or paralegally, required studies or documents such as Environmental Impact Reports (EIRs), Environmental Impact Statements (EISs), etc. (Erickson 1979, p. 194).

Environmental impact assessment usually is defined broadly as objective and subjective cataloging of the total physical

and bioligical effects of a proposed development (Munn 1975, p. 8). We prefer a narrower meaning such as that given by Lash et al. (1974, p. 10): "The process of doing predictive studies on an action and analyzing and evaluating the result...".

Background to Environmental Impact Assessment

Environmental impact assessment is a distinct and expanding field of applied ecology, but methods for assessing environmental impact are still developing.

> "Environmental science, today, is unable to match the needs of society for definitive information, predictive capability, and the analysis of environmental systems as systems. Because existing data and current theoretical models are inadequate, environmental science remains unable in virtually all areas of application to offer more than qualitative interpretations or suggestions of environmental change that may occur in response to specific actions" (National Science Board 1971, in Matthews 1975, p. 124; see also White 1980).

Furthermore,

> "Although the institutional procedures to be followed in the assessment process have been formalized in a number of countries, the scientific basis for these assessments is still rather uncertain" (Munn 1975, p. 8; see also Fischer and Davies 1973a).

Van Winkle et al. (1976, p. 247) succinctly state the frustrations of many who are involved in e.i.a.:

> "...ecologists cannot help but become acutely aware of the limitations in the 'state of the art' of impact assessment...when they are asked to play substantive roles in a decision-making process which stands at the controversial interface between industrial or economic progress and environmental protection."

Additional evidence that e.i.a. methods are only developing can be seen in the literature. Most publications dealing with methods of e.i.a. appear as in-house publications and books rather than in primary scientific journals (e.g. bibliographies in Fischer 1974; Matthews 1975; Warner and Preston 1973, in Munn 1975). Peterson (1974) identifies the indiscriminate combination of moral–political questions (e.g. What quality of environment do we want?) with scientific ones (e.g. How long will it take for a stream to recover from an oil spill?) as one of the problems retarding the development of adequate methods.

Scientific assessment of environmental disturbance in aquatic environments is not a new endeavour (e.g. Hynes 1966). However, some differences exist between what used to be (and still is) the use of applied ecological approaches in assessing environmental disturbances and what we now term environmental impact assessment. For example, e.i.a. programs may have the following characteristics:

1) They are usually short-term studies.

2) They frequently involve many disciplines.

3) They are often large, covering extensive geographical areas, involving many people, and incurring considerable costs (e.g. The Alberta Oil Sands Environmental Research Program was scheduled to spend ≃$4 million/yr evaluating the effects of tar sand development in northern Alberta).

4) They usually involve several different levels of government, universities, consulting firms and other agencies.

5) They are often crisis-oriented, reactive and *ad hoc* in nature.

6) Information generated by e.i.a.'s has a greater-than-ever chance of being used in development decisions in today's environmentally conscious world.

Development of a legal (or paralegal) framework for e.i.a. is relatively recent. Public involvement in environmental issues peaked in the late 1960s and early 1970s (Sandbach 1978; Parlour and Schatzow 1978) resulting in passage of the National Environmental Policy Act (NEPA) in the USA. The formal adoption of an e.i.a. process in the USA strongly influenced the rest of the western world to follow suit with similar programs (Wathern 1976; Kettle 1977; Lang and Armour 1977; Lee and Wood 1978). NEPA and the Canadian Federal Environmental Assessment and Review Process (E.A.R.P.) are only small parts of environmental law/policy in the USA (Wagner 1977; Bufford 1978) and Canada (Kettle 1977), but they are the pertinent actions regarding e.i.a.

Background on environmental legislation and/or government policy relevant to e.i.a. can be found in the following publications:

United States — Favorable commentaries on NEPA have included overviews of the legislation (e.g. Anderson 1973, 1974; Liroff 1976), its use (e.g. Coggins 1972), and numerous case studies of agency compliance (e.g. Andrews 1976). Subsequent criticisms of NEPA implementation (e.g. Sax 1973; Bardach and Pugliaresi 1977; Fairfax 1978) led to new regulations to improve the NEPA process (Liroff 1980). More recent analyses of NEPA reveal a better understanding of environmental problems, their solution, and administrative reform (e.g. Ingram and Ullery 1977; Fairfax and Andrews 1979). Liroff (1980) provides an overview of NEPA's first decade. Numerous states have also enacted environmental laws similar to NEPA (Yost 1973; Wandesforde-Smith 1977).

Canada — Kettle (1977) and Emond (1978) describe Canadian federal, provincial, and municipal law/policy relevant to e.i.a. Hurtubise (1977), Federal Environmental Assessment Review Office (F.E.A.R.O.) (1979), and Emond (1978) describe the Canadian Federal Environmental Assessment and Review Process (E.A.R.P.), and Emond (1978) provides a critical review of E.A.R.P. Federal Activities Branch Environmental Protection Service and Federal Environmental Assessment Review Office (1978) presents guidelines for E.A.R.P.

There is controversy in Canada over whether or not a requirement for e.i.a. should be statutory, as in the USA (see Environment Protection Board 1973; Lucas 1973; Lash et al. 1974; Templeton 1974; Emond 1978). In fact, e.i.a. authority exists under current federal and provincial statutes, but the effectiveness of these provisions is limited by various constraints (Lucas 1973, 1974). The cautions of Hedgpeth (1973, p. 442), Van Winkle et al. (1976, p. 252), and Erickson (1979, p. 360) are appropriate in this regard. A comment by

Emond (1978, p. 271) is pertinent here: "Whatever one may say about environmental impact assessment, its success is more related to the people who administer the process and the politicians, and has very little to do with the existence or non-existence of legislation."

Other western-world countries — Several countries have adopted procedures for EISs (e.g. Australia, France, Ireland), some have powers to require a type of e.i.a. (e.g. West Germany, Denmark), and others are actively assessing the value of e.i.a. systems (e.g. The Netherlands, U.K.) (Lee and Wood 1978; Sandbach 1978; see also Bisset 1980). Most western-world countries have chosen regulation rather than legislation. The context of e.i.a. in the USA is different than in Europe so that the workings of the USA system may not give much guidance to the likely effects of e.i.a. systems in European countries (Bisset 1978; Lee and Wood 1978). See Lundqvist (1978) for a comparison of responses to demands for environmental policy and the successes of adopted policy in open, conflict-oriented, and closed, consensus-oriented political systems.

It should be noted that, while a formal e.i.a. process may serve to preserve and protect ecosystems, continuation of such benefits may eventually depend on our ability to predict and evaluate effects of impacts rather than on "environmental action" (Eberhardt 1976, p. 67).

The "Ideal" Environmental Impact Assessment

Review of Existing Methods

A need to develop adequate methods for e.i.a. has been repeatedly identified by many authors (Andrews 1973; Fischer and Davies 1973a; Jordan 1973; Peterson 1973; Fischer 1974; Fischer and Francis 1974; Duffy 1975; Munn 1975; Coleman 1977). Administrative requirements (non-statutory and statutory) to do e.i.a.'s have been adopted far in advance of our capabilities to actually do them. Unfortunately, these requirements do not offer adequate methods nor do they suggest what criteria for assessment should be used (Fischer and Davies 1973a; Sondheim 1978). Adding to the confusion, in recent years the concept of environment has been broadened to include socioeconomic parameters (e.g. Burchell and Listokin 1975), as well as the traditional ones in the physical and biological sciences.

Publications have proliferated in response to the need for adequate methods in e.i.a. (see reviews in Burchell and Listokin 1975; Munn 1975; Skutsch and Flowerdew 1976; Canter 1977; Coleman 1977; Sondheim 1978; Bisset 1980). The methods used in such publications can be classified according to the kinds of techniques used or according to their intended function (Skutsch and Flowerdew 1976):

Form — This includes six main techniques (Munn 1975; Skutsch and Flowerdew 1976; Sondheim 1978): panels, checklists, flow diagrams,[1] matrices, overlays, and modeling (Table 1), but there can be overlap between them (e.g. the Battelle indexed matrix method uses panels). Munn (1975, table 4.5), Coleman (1977, table 1), and Bisset (1980) critically compare and evaluate contemporary methods (see also Canter 1977, tables 10-7 and 10-8).

Function — Skutsch and Flowerdew (1976) identify techniques designed to help identify probable impacts of alternative projects (impact identification) (e.g. flow diagrams, matrices); to assess/quantify probable impacts of alternative projects (impact evaluation) (e.g. matrices); and to compare impacts of alternative projects and select the least damaging one(s) overall (impact comparison) (e.g. matrices, overlays, modeling). This third group may include the previous two.

Although these methodologies exhibit some desirable features, none represent a panacea (Skutsch and Flowerdew 1976; Coleman 1977; Gilliland and Risser 1977). Most contemporary methods share common faults and problems:

1) They attempt to be all-inclusive. It is unlikely that a single method will be able to bring together detailed information on disparate topics successfully (e.g. Bisset 1978, p. 45). Furthermore, no single method can evaluate total impact; compare alternatives; organize, summarize, and synthesize the tremendous amount of information usually generated in an impact study; and then precisely communicate pertinent data to appropriate users (Coleman 1977; Gilliland and Risser 1977).

2) Quantitive values are rarely used. Assigning relative numerical values to potential impacts is less useful than actually quantifying estimates of effects.

3) Formats may be too rigid. Types of environmental information can vary but the method of using e.i.a. techniques is fixed (e.g. matrices). Even factors which do not lend themselves to the treatment have to be adapted to fit into it. Thus, a more flexible system is required.

Bisset (1980) has predicted a trend away from the use of complex numerical methods for e.i.a. and toward the use of approaches which provide qualitative, descriptive, and disaggregated information, as decision-making becomes more politicized.

Traditional research strategies using the scientific method appear to have been largely overlooked in the rush to satisfy requirements for environmental legislation, and many workers are beginning to realize this (e.g. Keeney and Robilliard 1977, p. 165). The scientific method can provide the desired quantification while remaining flexible because a rigid format for it does not exist. We do not propose that the scientific method is a panacea. In fact, it is not the answer to doing a wide-ranging e.i.a.; no single method is. However, even a large-scale e.i.a. could be composed of specialized research groups using the scientific method and contributing incrementally to an overall body that can synthesize their research into meaningful predictions of impact (e.g. Berger 1977a, b; Abrams and Primack 1980).

Elements of an "Ideal" Environmental Impact Assessment

Here, we propose the elements that constitute an ideal e.i.a. (adapted from Rosenberg and Snow 1977) and consider their relevance using literature on the philosophy of e.i.a.

[1]Terminology according to Munn (1975); = "linear graphs" of Skutsch and Flowerdew (1976) and "networks" of Gilliland and Risser (1977).

TABLE 1. Summary of methods for doing environmental impact assessments (e.i.a.'s).

Method	Panels (and workshops)	Checklists	Flow diagrams	
Examples	Sondheim (1978), Love et al. (1975) (see also "Battelle method"; Holling (1978))	Hagan and Roberts (1971) Henwood (1971) Burchell and Listokin (1975)	Sorensen (1971 in Munn 1975, p. 44) Van Winkle et al. (1976) Skutsch and Flowerdew (1976)	Leopold et al. (1971); Environmental Research and Counsel (1973); Fischer and Davies (1973a); Fischer and Francis (1974); Parker and Howard (1977); Federal Activities Branch Environmental Protection Service and Federal Environmental Assessment and Review Office (1978)
Use	To choose between project alternatives (including no-go). Recommended as a guideline only and not as an ultimate decision algorithm (Sondheim 1978)	To broadly list possible consequences of a proposed action in order to: 1) Recommend methods of investigation 2) Standardize inputs 3) Provide consistency (predictability, replicability) in topic coverage (Munn 1975; Burchell and Listokin 1975)	To identify action — effect relationships (Munn 1975)	To assess impacts associated with almost any type of activity by assessing interactions between environmental setting and proposed action (Munn 1975; Gilliland and Risser 1977; Sondheim 1978)
Description	A number of separate panels: 1) List project alternatives and environmental aspects to be considered; 2) Rate each aspect of all alternatives; 3) Weight each aspect. Favored alternative is obtained by multiplying ratings and weightings (Sondheim 1978). See Love et al. (1975) for Delphi method and Dee et al. (1973) for Battelle method. *Workshops* (Burchell and Listokin 1975) use an assemblage of experts to investigate aspects of the environment and could be considered a type of panel. Usually deal with a specific area of e.i.a.	Comprehensive lists, perhaps hierarchical of items to be considered in evaluating environmental impact (Munn 1975, Gilliland and Risser 1977)	Steps of actions/effects connected by direction indicating arrows to show sequences of events. These causal chains can indicate overall effect of a development. Basic organization: by land-use types (Skutsch and Flowerdew 1976; Gilliland and Risser 1977)	An extension of the checklist. One axis describes the proposed action, the other axis lists environmental conditions. Cells in the matrix can numerically indicate impact magnitude, importance, probability, time scale, etc. (Munn 1975; Gilliland and Risser 1977; Parker and Howard 1977)
Strengths	1) Cheap and fast 2) A large number of alternatives can be handled 3) Ease of reassessment, if necessary 4) Direct public participation possible 5) Can incorporate other methods as part of panel's work (Sondheim 1978)	1) Stimulates broad thought about possible impacts 2) Can ensure significant items are not omitted (Munn 1975, Gilliland and Risser 1977)	1) Permits visualization of connection between action and impact and immediate identification of causal elements 2) Simplifies overall effect because impacts are organized according to land use 3) Organizes action–effect impact chains so they can evolve into a matrix or models with further study and quantification (Munn 1975; Skutsch and Flowerdew 1976; Gilliland and Risser 1977)	1) Provide helpful initial guidance in designing further studies 2) Inexpensive 3) Highly visual. Communicates well (helpful to decision-maker) 4) Convenient and comprehensive 5) Allow comparison of seemingly incomparable events 6) Allow comparison of relative importance of each impact (Kefalas and Pittenger 1975; Munn 1975; Skutsch and Flowerdew 1976; Jackson et al. 1978; Sondheim 1978)[a]
Weaknesses	1) Tends to be too subjective; i.e. a) results will depend on composition of the panels b) selection of panel members is difficult especially because of the non-replicability of rating schemes (Sondheim 1978) c) aspects of environment chosen may not be important 2) Attempts to be too all-inclusive but: a) only deals with choice of alternatives, a small part of e.i.a. b) does not consider interactions (Sondheim 1978) 3) *Workshops* — Analysis overall is frequently uneven; some impacts receive detailed attention while others do not (but see Holling 1978)	1) Static and non-quantitative: give no idea of degree or magnitude of impacts or of probable interactions 2) Impact *in toto* not considered 3) More descriptive than comparative (Burchell and Listokin 1975; Gilliland and Risser 1977)	1) Identification of major types of impact not facilitated 2) Not recommended for large regional actions; best suited to single project assessments because displays (for the former) may become so extensive (especially when alternatives are considered) that they are useless 3) Usually are not quantitative 4) Not comprehensive and usually do not have feedback capabilities 5) Can be subverted to display the management of e.i.a.'s (Munn 1975; Kefalas and Pittenger 1975; Van Winkle et al. 1976; Gilliland and Risser 1977)	1) Visually, can be overwhelming if large numbers of cells are involved (e.g. when alternatives are considered). Unwieldy volumes of data in a relatively compact format may make it too difficult to assess overall impact by inspection 2) Interdependency among impacts (i.e. interactions) ignored. Only relationship between initial action and its terminal effects considered 3) Numerical estimates are subjective. There is no objective procedure to ensure comparability between impacts. Only ordinal conclusions can be used. Summarization is conceptually difficult 4) Too much is attempted; no quantification involved (Jowett 1972; Sorenson 1972; Fischer and Davies 1973a; Burchell and Listokin 1975; Skutsch and Flowerdew 1976; Gilliland and Risser 1977; Jackson et al. 1978; Lee and Wood 1978; Sondheim 1978)[a]

TABLE I (*Concluded*)

Method	Matrices (continued) — indexed	Overlays	Modeling
Examples	Battelle method — Dee et al. (1973)	McHarg (1971), Rattray et al. (1973)	Walters (1974, in Munn 1975) Gilliland and Risser (1977) Holling (1978) Ogawa and Mitsch (1979) Carter et al. (1979)
Use	For quick and rough estimates of impacts of water resource developments (Burchell and Listokin 1975; Munn 1975; Sondheim 1978)	To choose the most suitable location for project siting by demonstrating differences in impacts and costs as a function of variation in land characteristics (Burchell and Listokin 1975; Gilliland and Risser 1977; Sondheim 1978)	Potentially the most worthwhile method because of its predictive capabilities, use of large amounts of (quantitative) data, and its capability to identify additional research needs
Description	A matrix method which focuses on specific environmental quality components chosen for relevance to project alternatives under consideration	The study area is subdivided into geographical units, and social and physical parameters assumed to affect land use are mapped on transparencies. Relative numerical weights may be assigned to each parameter. Areas (grid cells) possessing preferred combinations of parameters (social and physical characteristics) are determined by overlapping the transparencies. Computer maps can be used instead (Munn 1975; Gilliland and Risser 1977; Sondheim 1978)	Simplified representations of reality utilizing mathematical representations to link physical, ecological, and sociological effects (Munn 1975)
Strengths	1) Public participation built in at several stages 2) Results weighted according to importance and divisible into short- and long-term impacts: a) values allocated over range of possible impacts b) uses ranges for parameters c) individual biases minimized when choosing "important" environmental components d) decision maker helped in quantifying value judgments 3) "Red flags" indicate areas of further study needed due to insufficient data or unacceptable values 4) Job of analyst simplified (e.g. use of ranges for parameters, red flags, assessment trees) (Burchell and Listokin 1975; Munn 1975; Skutsch and Flowerdew 1976; Sondheim 1978)	1) A simple means to obtain quantified, comparative and aggregative measures of impact: a) best combination of land-use suitability, engineering feasibility, and compatibility of action can be evaluated b) illuminates complex spatial relationships c) process can be computerized to aggregate predicted impacts and choose least affected areas 2) Qualitative and quantitative data can be used (Burchell and Listokin 1975; Munn 1975)	1) Requires commitment to be made at start of e.i.a. 2) Requires quantitative definition of essential elements of assessment and relationships between the elements 3) Can handle large volumes of data and complicated linkages between physical, ecological, and social studies. Consequences of many options can be investigated 4) Assumptions must be checked carefully because every link must be defined 5) Ranges of effects can be checked 6) Macroscale models can identify needs for additional research which are then dealt with in detail by microscale models (Munn 1975; Gilliland and Risser 1977)
Weaknesses	1) Composition of weighting panel a problem. "Delphi" method of choosing relative importance of environmental components (i.e. iterative judging by members of a panel until consensus obtained) minimizes individual bias but the panel could become polarized 2) Time consuming 3) Expensive 4) Ignores interdependency of impacts 5) Value judgements pervade the methodology. Best choice of environmental quality components to be evaluated not always obvious. Importance of incremental changes in the environment are prejudged 6) Scoring algorithm fairly inflexible; may be unsuitable to evaluate some components (Burchell and Listokin 1975; Munn 1975; Skutsch and Flowerdew 1976; Sondheim 1978)	1) Factor interdependency not considered 2) Usually restricted to environmental characteristics already mapped 3) Use of large numbers of factors results in difficult choices 4) Only ~10 overlays can be used effectively 5) Not useful if location is already chosen and/or if the real problem concerns the type of feature to be constructed (Munn 1975; Skutsch and Flowerdew 1976; Sondheim 1978)	1) Expensive (labor, time, cost) 2) Output quality depends on input quality. Links must be identified and explicitly defined 3) Still embryonic in e.i.a.'s. Successful models notably lacking. Of doubtful routine application to e.i.a. because of certain analytical and informational limitations (i.e. levels of analysis and synthesis required for in-depth study exceed capabilities of agencies responsible for e.i.a.'s) (Munn 1975; Sondheim 1978; Ogawa and Mitsch 1979; Carter et al. 1979) Criticisms specific to energy models of Gilliland and Risser (1977): 1) Not all impacts can be defined in energy terms (e.g. groundwater contamination) 2) No absolute assurance that important pathways and interactions have been identified 3) Cannot deal with differences in value systems 4) Interpreting magnitude of impact depends on how the system is bounded initially, something the method cannot tell you how to do 5) Requires relatively "simple" systems (e.g. desert) 6) Requires much background, energetic data

[a]See also Holling (1978, table 5.2, p. 76) for advantages and disadvantages of Leopold matrix.

1) Definition of scientific objectives — This should always be the initial step taken in scientific research. Peterson (1973, p. 389) has identified why this step is also pertinent to e.i.a.: "Proposals to construct one or more pipelines from the north bring into focus several subjects that are not so much 'pipeline problems' as they are *problems of defining scientific work objectives* [our italics] that will be of use to those who must decide whether these proposals for technological developments are acceptable."

2) Background preparation — Familiarization with what to expect is important, as for any research project. The following aspects are included: literature reviews of similar projects, case history studies of natural and man-made occurrences similar to the ones being considered, and reconaissance of the proposed project site.

3) Identification of main impacts — Choice of only *major* impacts for study is justified because of the impossibility of studying *all* impacts given the usual funding and time constraints and deficiencies in ecological knowledge (Nielsen et al. 1973; Abalu 1976; Brink 1978; Lee and Wood 1978; Cole 1979). Potential implications of a failure to limit studies are stated by Petr (1978, p. 380) in his review of tropical, man-made lakes:

> "It is also true that many scientists still believe that a decision can be based only on absolute, or near to absolute knowledge. That this attitude is not always in the interest of environment is well known from the fisheries where the absolute proof of decline in fish stock is its total disappearance."

Hopefully, significant secondary and tertiary effects as well as the immediately visible primary effects (terminology according to Peterson 1973) also can be identified.

4) Prediction of effects — The essence of e.i.a. is the prediction of effects (during the preproject phase) and then measurement of the deviation in the state of the ecosystem with and without the impact (see "Monitoring and assessment," below) (Dee et al. 1973; Van Winkle et al. 1976; Gilliland and Risser 1977; see also Erickson 1979). Ideally, this would include some estimate of the reliability of the predictions (Erickson 1979). There are three basic methods available to do this: field surveys, experimental manipulation (both inductive methods), and modeling and computer simulation (a deductive method) (Goodall 1977).

Surveys — These provide lists of species. Those that will be detrimentally affected by an impact can be identified (e.g. endangered species).

Experimental manipulation — This allows control of some variables while others are altered. This technique is particularly effective in testing hypotheses of probable effects arising from the identification of main impacts and leading to predictions of these effects (Rosenberg and Snow 1977). For example, proposed actions could be simulated on a portion of the system to be affected or on a smaller, comparable system (Ward 1978).

Modeling — Modeling techniques such as computer simulation can be extremely powerful in holistic approaches but are only as strong as the assumptions and data that are used.

Optimally, all three techniques would be used in e.i.a. Obviously, there is no ". . . grand strategy . . . based on specific tactics perhaps practicable only in special instances" (Moore 1978) so it is important to consider a number of approaches to pollution/impact assessment (Edwards and Goodman 1972; Lewis 1978; Moore 1978). Table 2 summarizes some of the problems associated with using each of the three techniques and suggests possible solutions.

5) Formulation of usable recommendations — Information generated by an e.i.a. should be usable in decision-making. Predicted effects should be related to the actual decision of whether or not to proceed with the project or to adopt alternatives. If the decision is made to proceed, the e.i.a. should provide input into the design of the project or its alternatives and it should be useful in minimizing adverse effects.

6) Monitoring and assessment — Measurement and interpretation of environmental effects during and after the project has been completed may be the most important element of e.i.a. because it can be used to determine the value of techniques used and accuracy of predictions made (Munn 1975; Coleman 1977; Dorney 1977; Holling 1978; Lee and Wood 1978; Engelmann 1979; Horak and Olson 1980); identify secondary and tertiary effects; provide case history information for use in other, similar e.i.a.'s (Horak and Olson 1980); and assess directional change (Fischer and Francis 1974). Monitoring provides the experience and data necessary to advance the scientific basis for e.i.a. (Fischer and Francis 1974; Munn 1975; Holling 1978). Monitoring and assessment depends mainly on surveys (i.e. comparison of preoperational and operational data), but can also be used to sharpen predictions of future effects made by simulation models (e.g. Thomas et al. 1978) (Table 2).

The elements discussed above have been combined to exemplify what we would describe as a scientific approach for doing e.i.a.'s (Fig. 1). The process requires continued interaction among the elements (e.g. Matthews 1975, p. 123). Ideally, the process would progress (over an increasing gradient of difficulty in time, space, and level of biological organization) from predicting and assessing short-term, site-specific, individual effects to long-term, widespread, ecosystem level effects (Van Winkle et al. 1976, fig. 1).

Twelve publications containing philosophical treatments of the design of e.i.a.'s (mostly the broad definition, see above) were chosen to test the relevance of the proposed elements. Authors included a forestry scientist, law professor, economist, engineers, and government administrators, and provided a broad cross section of views. Each paper was examined for at least some indication of each element using four assessment categories: agreement with the element, disagreement, no specific mention, and contradictory statements (Table 3). Admittedly, the analysis has two shortcomings. First, it is at least partly subjective. Since differences in meaning are hard to avoid, some second-guessing was involved, but each paper was carefully scrutinized before assessments were made. Second, even though the backgrounds of the authors are diverse, there should be broad agreement with the

TABLE 2. Summary of problems and possible solutions of using surveys, experimental manipulation, and modeling for prediction and monitoring/assessment in environmental impact assessment (e.i.a.).

Technique	Problem	Possible solution(s)	Comment
Surveys[a]	1) Prediction of effects of an impact on species based solely on qualitative data	Thorough knowledge of life history of the species involved	The preparation of "lengthy laundry lists" of species (Andrews 1973, p. 198) does not help in predicting effects unless qualitative information is used in a circumstantial fashion to predict change (e.g. a silt-sensitive species will be driven away by increased sedimentation as a result of highway construction). (See also Holling 1978; Ward 1978)
	2) Monitoring and assessment a) Lack of true replication (Eberhardt 1976)	Use the "pseudodesign" proposed by Eberhardt (1976) (see also Green 1978). Aggregate a number of sites into one study (regional approach) (Eberhardt 1976)	The pseudodesign proposed uses "...preoperational data on a site and a control area contrasted to post-operational data on both areas, and substituting replication in time for true replicate areas" (Eberhardt 1976, p. 27). "...Its main value may be in focusing attention on just how few real data points are generated by, say, two years of 'baseline' and two years of 'operational' study" (Eberhardt 1976, p. 35)
	b) High numbers of samples required (Eberhardt 1976; Baker 1978)	Do what is possible. Adjust precisions and confidence intervals accordingly. Or: simplify by sampling selected species (Resh 1979; Gray 1980) or using population phenomena other than density (Holling 1978)	Probably only major changes will be detected using contemporary sampling techniques and with the large variabilities involved. Prohibitively high numbers of samples are required to detect even large changes (Eberhardt 1976; 1978). Baker (1978, p. 448): "...with less than those numbers of samples [5–10 grab samples per sampling station] it is not possible to prove anything other than catastrophic changes." [But see the suggestion of Gray (1980, p. 65) for a "...rationalized program" and the strategy of Holling (1978, p. 282–285)]
	c) Isolating sources of variance. Statistically significant changes may be due to natural variation, the impact itself or other sources of pollution/disturbance (Pella and Myren 1974; Eberhardt 1976; Myren and Pella 1977; Cooper 1978; Moore 1978; Penrose 1978; Gore et al. 1979; Gray 1980)	Attempt to isolate sources of variance by adequate design. Adequate replication of samples [see (b), above]. Potential impacts from other sources should, at least, be considered (Gore et al. 1979)	See Myren and Pella (1977, p. 371). Additionally, long-term monitoring may reflect long-term trends that may differ in control and impacted sites (Eberhardt 1976; see also Lewis 1980). Long-term monitoring does have general support (e.g. Myren and Pella 1977, p. 372; Baker 1978, p. 448; Livingston 1980, p. 21; see also Wiens 1977)
	d) Monitoring only provides circumstantial evidence on cause and effect (Baker 1978). In fact, separation of cause and effect is rarely unequivocal (Munn 1975; Eberhardt 1976; Goodall 1977)	Use of direct experimentation (see below). Or: knowledge of life history of species (Gray 1980)	Baker (1978, p. 448): "Monitoring measures trends but does not explain them. Even good correlation between pollutant and biological data does not prove a cause-and-effect relationship." (But see Gray 1980.) Strong but still circumstantial evidence is provided by historical monitoring (e.g. Starrett 1971; Edwards and Goodman 1972; Pyle and McCarthy 1973; Resh and Unzicker 1975; Van Der Schalie 1975)

TABLE 2 (*Continued*)

Technique	Problem	Possible solution(s)	Comment
	e) Standardizing sampling designs/ methods in pre- and post-impact studies (Austin 1976; Thomas et al. 1978; Gore et al. 1979)	Do not change a sampling program, once implemented, until interrelationships between old and new methods/procedures are established (Gore et al. 1979)	Gore et al. (1979, p. 6): "...Once a well-designed sampling program is implemented, only changes that can reasonably be expected to improve the quality of data needed for impact evaluation be allowed" *Additional comment* — See Gray (1980) for definitions of "monitoring". Moore (1978): "Monitoring aims and methodologies await a rigorous general synthesis." (See also Lewis 1978)
Experimental manipulation[b]	1) Need to encompass a large scale spatially and temporally (Goodall 1977) 2) Sufficient replication (Goodall 1977)	Use regional approach (cf. Eberhardt 1976) Adequate experimental design (including, perhaps, a regional approach; see Goodall 1977)	Goodall (1977, p. 314): "...The sound experiment on natural ecosystems not only needs to be replicated over the whole areal range to which results are to apply, but also the replicates should be started in different years, so that collectively they will explore the interaction between seasonal conditions and variation in the initial state of the system in determining the course of change"
	3) Require large amounts of money, time, and effort. Administrative and financial problems may impede long-term manipulative studies (Eberhardt 1976; Goodall 1977; Cooper 1978)	Make the commitment and then use studies such as the Experimental Lakes Area, Ontario, and the Hubbard Brook Experimental Forest, New Hampshire, as models	These examples may be exceptions that prove the rule! The importance of a whole watershed approach is discussed by O'Sullivan (1979). Goodall (1977, p. 314): "But the amount of effort for a well-designed experiment of this sort is very large. It needs a very firm organization; and the fact that observations need to continue for several years means that only well-established institutions which are in a position to plan for ten years or more ahead could undertake such an experiment with any hope of bringing it to a successful conclusion." Considerations of money, time and effort aside, the establishment of experimental watersheds to operate simultaneously in different regions would be a powerful tool in studying cumulative impacts on a regional or national scale (see text) *Additional comments* — Experimental manipulation may be the most important of the three predictive techniques, but deliberate modification of an ecosystem to observe consequences is rare (Peterson 1973). Eberhardt (1976, p. 32): "An important potential for effective experimental design exists whenever it is possible to somehow manipulate possible sources of damage." It may be awhile before adequate models are developed so ecological hypotheses should be tested by direct experimentation (Cooper 1978)
Modeling and computer simulation[a,c]	1) Mathematical and computer expertise (not always available to an e.i.a. team) is necessary	Make necessary expertise a priority	

TABLE 2 (*Concluded*)

Technique	Problem	Possible solution(s)	Comment
	2) Requires advance commitment for assembly and organization of information in model development (Munn 1975; Van Dyne 1978)	Do it	Identified as a strength in Table 1
	3) Relevance of the behavior of the model to behavior of the real life system (Goodall 1977; Swartzman 1979; see also Shaeffer 1980). There is a lack of knowledge of the structural details in ecosystems (Eberhardt 1976; Foin and Jain 1977; Thomas et al. 1978; see also Carter et al. 1979; Hunter 1979; Ogawa and Mitsch 1979)	More emphasis on the study of structural features (e.g. life histories of species; see Rosenberg 1979) rather than numbers (Holling 1978). Subjective validation (Hunter 1979)	Modeling is still in its infancy as a tool in e.i.a. and it may be awhile before adequate models are developed
	4) "The explainable phenomena are limited by the variables included and not included in the model" (Swartzman 1979, p. 160)	Use of causal links (Swartzman 1979)	
	5) Lack of attention to sampling and estimation problems (Eberhardt 1976)	More attention to these problems	
	6) The need to complete the model sometimes hides the gaps in knowledge and research needs identified by the model (Eberhardt 1976)	Regard modeling as a tool rather than an end in itself	An excellent way to identify gaps in knowledge and research needs (Eberhardt 1976; Ward 1978)
	7) Monitoring long-term predictions and judging scientific and societal acceptability of predicted changes (Auerbach 1978)		Most valuable potential use of models is predicting long-term effects (e.g. Shugart and West 1977 in Auerbach 1978) *Additional comment* — Van Dyne (1978, p. 191): "...Models are not a utopia. Models do not replace all other approaches to dealing with complex problems. Models are simply a supplement to other approaches we will need for more intensive decision-making in resource management. Present models are most useful in predicting order-of-magnitude or directional, qualitative responses rather than providing hard-and-fast dictates or specifying absolute requirements for renewable resource decision-making purposes." (See also Thomas et al. 1978)

[a]For prediction, monitoring and assessment.
[b]For prediction.
[c]See also Table 1.

proposed elements if these elements are universally applicable (except for those elements which are specific to research).

Table 3 indicates there is general agreement with the proposed elements (42 times out of a possible 72, equaling 58%). Outright disagreement and contradictory statements were not major factors (3 and 4%, respectively). Failure to mention an element was common (35%), but this was not surprising because the papers were not structured to consider specifically the proposed elements. There was overall agreement with the need for identification of the main impacts and prediction of the effects of these impacts. One or more predictive techniques was mentioned frequently. The use of recommendations in the decision process was unanimously endorsed. Clear agreement was not apparent for definition of scientific objectives, background preparation, and monitoring and assessment, probably because these elements are specifically research- or design-oriented. Perhaps, because of the wide mix of backgrounds of the authors, this result is not surprising. Authors with a scientific background tended to agree with the six elements more than authors with other backgrounds. Still, in view of the importance of monitoring and assessment to e.i.a., exclusion of this element by half of the papers is surprising. None of the papers that emphasized e.i.a. as part of a planning process (Flamm 1973; Plewes and Young 1973; Fischer 1974; Duffy 1975) excluded monitoring and assessment.

Additional elements important to e.i.a. were identified from the publications reviewed and in our discussions:

Sufficient lead time — This need was identified by 11 out of 12 papers (see also Fischer and Davies 1973a; Jordan 1973; Fischer and Francis 1974; Jones 1974). Environmental impact assessment should be an integral part of planning and should be done simultaneously with engineering and economic studies rather than being "reactive" (Holling 1978, p. 1, 6, 16; see also Erickson 1979).

Public participation — This was identified by three-quarters of the papers as an integral part of e.i.a. (see also Jordon 1973; Jones 1974; Templeton 1974). "Public" is defined, in general, by Canter (1977, p. 223, 227) and by Abrams and Primack (1980, p. 16–17) with regard to radioactive waste management controversies. The public often makes observations useful to scientists, and public perceptions can help in making value judgments (Canter 1977; Brink 1978; Erickson 1979, 1980; Abrams and Primack

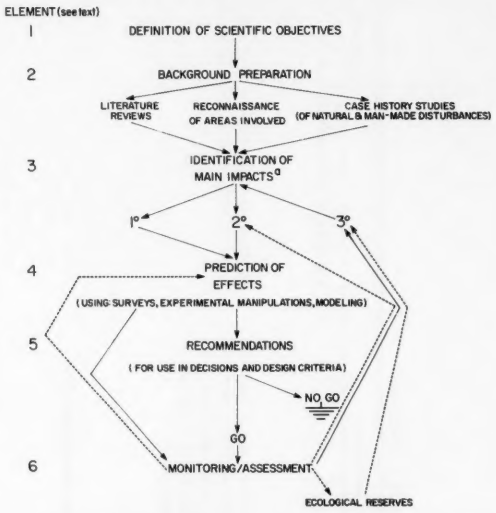

FIG. 1. A scientific approach to environmental impact assessment. (Assumes adequate lead time. Broken lines represent uncertainty. [a]Including those of alternative projects.)

TABLE 3. Analysis of philosophical publications on design of environmental impact assessments for agreement with proposed elements.

Reference	Definition of scientific objectives	Background preparation	Identification of main impacts	Prediction of effects	Formulation of usable recommendations	Monitoring and assessment	Totals[a] X √ Δ ?	Overall indication of paper (≥3)
Andrews (1973)	Δ	Δ	√	√	√	Δ	0 3 3 0	√Δ
Environment Protection Board (1973)	√	√	?	√	√	√	0 5 0 1	√
Fischer and Davies (1973b)	Δ	Δ	√	√	√	Δ	0 3 3 0	√Δ
Flamm (1973)	√	Δ	√	Δ	√	Δ	0 3 3 0	√Δ
Peterson (1973)	√	√	√	√	√	√	0 6 0 0	√
Plewes and Young (1973)	Δ	Δ	Δ	√	√	Δ	0 2 4 0	Δ
Purple (1973)	Δ	√	√	√	√	√	0 5 1 0	√
Fischer (1974)	Δ	Δ	√	√	√	Δ	0 3 3 0	√Δ
Lash et al. (1974)	Δ	Δ	X	√	√	√	1 3 2 0	√
Lucas (1974)	Δ	Δ	√	Δ	√	√	0 3 3 0	√Δ
Duffy (1975)	Δ	Δ	?	√	√	Δ	0 2 3 1	Δ
Munn (1975)	X	√	?	√	√	√	1 4 0 1	√
Totals X	1	0	1	0	0	0		
√	3	4	7	10	12	6		
Δ	8	8	1	2	0	6		
?	0	0	3	0	0	0		
Overall indication of paper (≥6)	Δ	Δ	√	√	√	√Δ		

[a]X = disagreement, √ = agreement, Δ = no specific mention, ? = contradictory statement(s).

TABLE 4. Criteria used to assess contemporary environmental impact assessments. [The following treatment of each criterion was required for an optimal score (5). Criteria were scored lower (0–4) depending on how far they deviated from the stated conditions.]

I. Within the control of the scientist(s)
  1) Definition of scientific objectives
    Clear concise statement of scientific objectives at the beginning of the report
    Objectives directly related to evaluation of impacts of the proposed project (and alternatives) and site-specific
    Objectives suitable for hypothesis testing
    Statement of intent to produce predictive information and recommendations
  2) Background preparation
    Literature review — thorough but concise, pertinent to proposed project, includes basic research, effective and informative use of literature, good referencing
    Case history studies — critical use of data from similar projects or site-specific research, if available
    Reconnaissance (or actual survey) of the study area
    Use of expert advice, if applicable
  3) Identification of main impacts
    Major potential physical and chemical sources of impact identified (with justifications) and designated for analysis, construction, and operation of project considered
    Site/project-specific sources considered
    Long-term and cumulative sources considered
  4) Prediction of effects (on biota)
    Uses elements of background preparation
    Uses site-specific manipulative experimentation and/or modeling (to test hypotheses)
    Considers long-term and cumulative effects for the development being studied and other similar ones in the region
    Considers design alternatives
    Includes ranking of relative severity of effects
  5) Formulation of usable recommendations (for use in go/no go decision, alternatives and in design criteria)
    Logically derived from predictions (i.e. not simply a justification for the project)
    Directly applicable and site-specific
    Realistic
    Address long-term and cumulative effects
    Presence of specific recommendations for further research (if necessary)
II. External to the control of the scientist(s)
  1) Monitoring and assessment[a]
    Applicability and completeness of program
    Quality of data from actual monitoring during and after project completion
    Comparison of results with original predictions to test their validity
  2) Sufficient lead time
    Based on amount of time allowed to generate report but also considered length of field sampling period if it deviated markedly from total time allowed
    Two years = average score (3); score for more or less lead time depended on scope of development and the research needed to predict adequately effects of impacts identified for the project. In general, <1 yr represented inadequate lead time (at least to account for seasonal variation) and was scored low. Five years or more represented exceptional lead time and was scored high
  3) Evidence that recommendations were used in the decision (go/no go, alternatives) or design criteria
    Low score given for failure to incorporate realistic recommendations
    High score given for utilization of recommendations
III. Others[b]
  1) Public participation
    Inclusion of public in information-gathering processes
    Frequent public hearings, accessible especially to residents of affected area
    Opportunity for written comments/testimony provided; inclusion in report together with responses
    Evidence that significant public comments/suggestions were used
    Evidence of availability of report to public
    Sponsored early enough in decision-making process
  2) Adequate funding
    If dollar amount available, evaluated in respect to scope of project and extent of potential impact

[a]Timber management plans were scored 0 if they did not have or provide for a monitoring and assessment phase. Presumably, it is essential to know the effects of a management strategy.
[b]Elements that could belong to either of the previous two groups.

1980). Amateur naturalists outnumber professional ecologists and the amateur may accumulate valuable long-term information unavailable to the professional (Tips and Gysels 1979). Public participation also allows persons affected by a project to present their views, enhances administrative accountability, and allows active participation in the management of public resources (Lake 1973; Lucas 1973; Lash et al. 1974; Canter 1977; Erickson 1979, 1980; Abrams and Primack 1980). (Arguments against public involvement are given in Erikson 1980.)

Adequate funding — An ideal e.i.a. has adequate funding, although problems of defining adequate are obviously difficult. Environmental impact assessments usually total <1% of the total capital cost of a project and <10% of the feasibility study costs (Plewes and Young 1973; Munn 1975; Dorney 1977; see also Engelmann 1979).

Evidence that recommendations were used in the decision (go/no go, alternatives) or design criteria — This was added in our review because the relevance of e.i.a. is questionable if the recommendations produced are not used.

Contemporary Status of Environmental Impact Assessment

Methods Used in Our Review

Environmental impact assessments of many contemporary major activities and areas of development that involve aquatic resources were reviewed. The elements of an ideal e.i.a. identified above (see "The ideal environmental impact assessment") were defined in greater detail (Table 4) and were used as criteria in the review to score selected e.i.a.'s (see below).

Based on individual interests, we selected the following areas for analysis: steam electric power plants, fossil fuels (oil pipelines, coal, tar sands, and oil shales), recreation (camping, hiking, skiing, etc., developments and national park use master plans), reservoirs, wastewater treatment facilities, forestry (timber harvesting and spraying programs for insect pests), and estuarine impacts (dredging and water diversions).

Assessment teams were formed among the authors and a number of resources were used to obtain documents for review (Table 5). Predictive, preoperational studies of apparent high quality were sought. Some assessment teams had other *a priori* requirements as well: power plants — a diversity of fuels (nuclear, fossil) and habitats impinged (lakes, rivers, estuaries); fossil fuels, recreational developments, and forest insect spraying — largeness of scale and geographical extent; forest insect spraying — the most important forest insect pests; and wastewater treatment and estuarine impacts — broad geographical coverage. Monitoring and assessment studies (i.e. those conducted during and after completion of the project) were included, if available, but *post facto* studies alone were not accepted. Our intent was to select ≃ six published documents for each activity or area of development. One or two key documents per project within a development area were examined for scoring (see below) rather than trying to obtain and review *all* publications for that project. Searches for suitable documents to review usually lasted several weeks. A typical selection process is illustrated in Fig. 2. Documents chosen for review are described in Table 6.

Documents were thoroughly studied and each element was ranked on a 0−5 scale (0 = not done but should have been; 1−5 = poorly−excellently done). We defined a score of 3 as "average." The category "NA" was assigned if there was insufficient information available to grade the element or if the element did not apply. Only the numerical assessments were used in calculation of means.

Assessments were standardized as follows:

1) They were usually done separately by the members of an assessment team, individual assessments were then discussed, and a final mark given. Individual scores were generally the same, disagreements rarely exceeding 1 point on a criterion and 10−20% for a document.

2) Assessments by a team were presented to the group for general discussion, criticism, and, if necessary, rescoring.

3) One document from each development area was exchanged between teams for cross-assessment. Marks for

Table 5. Resources used to obtain documents for review.

Resource	Development area/Activity							
	Power plants	Recreation	Reservoirs	Wastewater treatment	Fossil fuels	Timber management plans	Forest insect spraying	Estuarine impacts
Abstracting services[a]	√			√	√			√
Bibliographies/literature citations in key documents	√			√	√	√		√
Personal communication	√		√	√	√	√		√
Library systems:								
University of California, Berkeley[b]	√	√	√	√	√	√		√
Berkeley Public Library		√						
U.S.E.P.A. Library, San Francisco	√	√	√	√	√	√	√	√
Pacific Gas & Electric Co., San Francisco, CA	√							
San Ramon, CA	√							
U.S. Forest Service, P.S.W. Forest and Range Experiment Station research library, Berkeley						√		

[a]For example, EIS, Environment Abstracts.
[b]Includes approximately eight libraries.

individual criteria were in agreement 63.6% of the time, differences of 1 point occurred 25.8%, and only one score differed by 2 points (1.5%). An "NA" was assigned five times (7.6%) when a score had been given in the original assessment; the reverse occurred once (1.5%). These errors were attributable to misunderstandings rather than disagreements between assessment teams. The good overall agreement in scoring indicates a fairly standardized approach and a high degree of replicability in the process.

Results and Discussion

In general, the search for relevant literature was hampered by the lack of a central source of documents and the generally low quality of the ones that were available. The number of documents chosen for review was only a small fraction of the number of titles perused ($\simeq<1-7\%$) and only 7–17% of the actual documents obtained (Table 7). Documents reviewed were judged the best available from a variety of sources (e.g. refereed journals, symposia, reports of contracted research, e.i.a.'s done to satisfy legal requirements, etc.). A limited number of documents of a lower quality than those normally accepted (and typical of those rejected) were included in the reviews done by the Wastewater treatment team (Onondaga Lake) and the Estuarine impacts team (Port Hueneme and Santa Cruz Harbor) for comparison with the best available documents. The Alsea study (Table 6) was chosen as a model of excellence for comparative purposes by the Forestry team. These extra documents were not included in calculation of mean scores.

Consideration of criteria — Criteria within the scientist's control (Table 4) were invariably assessable whereas the remaining criteria were less so (Table 8). "Monitoring and assessment" could be scored only $\simeq 1/3$ of the time (15 times out of a possible maximum of 44). The required information either was not included in the source documents (monitoring and assessment may not have been done) or the project may not have been started (or completed) when the document was prepared (e.g. the Mackenzie Valley Pipeline study). Source documents usually did not provide information on two criteria (Evidence that recommendations were used, Adequate funding) and these criteria could be scored only four times. They are not included in subsequent calculations.

Mean scores (±SD) for the eight remaining criteria indicate (Fig. 3) that the overall mean score of the best available e.i.a.'s (= 2.9 ± 1.3) does not exceed our defined average (= 3.0); but the overall mean score of the best available e.i.a.'s improves when legally required and publicity documents[2] are excluded from the calculations (= 3.4 ± 1.3). (Overall mean score of legal documents was only 2.4 ± 1.2.) This indicates that e.i.a.'s prepared to fulfill legal requirements or prepared as public relations documents are usually of lower quality than other e.i.a.'s. This can also be seen in a comparison of criteria evaluations of three report types for reservoirs (Fig. 4).

[2]Alberta Oil Sands Environmental Research Program (=A.O.S.E.R.P.) (1978) is a public relations document and has been included with the legal documents.

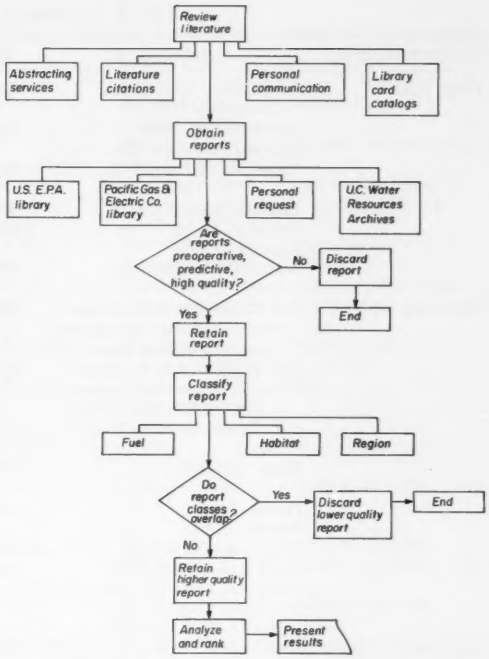

FIG. 2. Report selection process used in review of power plants (representative of process used in other development area reviews).

Only "Public participation" scored higher in legal e.i.a.'s, probably because it is required by the U.S. NEPA. The largest differences between nonlegal and legal documents occurred in "Definition of scientific objectives" and "Monitoring and assessment," both distinctly research criteria. The quality of critieria in legal documents tended to be more variable (C.V. = 50.0%) than in the other e.i.a.'s (C.V. = 38.2%). When legal e.i.a.'s were excluded from the calculations, the greatest increase in mean score occurred for "Monitoring and assessment." This suggests the greater importance of monitoring and assessment to other than legal types of e.i.a.'s.

Of the criteria within the scientist's control, lowest means were obtained for "Prediction of effects" and "Formulation of usable recommendations" (Fig. 3). We speculate that these are the hardest parts of an e.i.a. to do well.

Consideration of development areas — The quality of e.i.a.'s within and between development areas/activities, based on criteria within the scientist's control, varied greatly (Fig. 5). Overall mean scores (±SE) for each development area/activity indicated that studies fell into three broad quality groups: studies of above-average quality, including wastewater treatment [3.7 (±0.4)] and recreational developments [3.6 (±0.4)]; studies of approximately average quality, including estuarine developments [3.2 (±0.2)], power plant projects [3.1 (±0.4)], reservoirs [3.1 (±0.6)], and development of fossil fuel sources [3.0 (±0.4)]; and studies of below-

TABLE 6. Description of documents chosen for review.

Development/activity	Reference	Descriptor	Type of project	Location
Power plants	New England River Basins Commission (1971)	Seabrook	Nuclear	Hampton Estuary, New Hampshire
	Beer and Pipes (1968) Eiler and Delfino (1973)	Quad-Cities	Nuclear	Mississippi River, Illinois
	Ontario Hydro Co. (1977)	Atikokan	Fossil (coal)	Marmion Lake, Ontario
	Cole and Freeman (1972)[a]	Monroe	Fossil	Lake Erie, Michigan
	Fruh et al. (1974) Fruh (1977)	Ferguson	Fossil (gas, oil)	Lake Lyndon Baines Johnson, Texas
	Northern States Power Co. (1975)	Sherburne	Fossil (coal)	Mississippi River, Minnesota
Fossil fuels	U.S. Department of the Interior, Geological Survey and Montana Department of State Lands (1977)	Decker Coal	Surface mining of coal	Big Horn Co., Montana
	U.S. Department of the Interior, Bureau of Land Management (=U.S.D.I.B.L.M.) (1977a)	Northwest Colorado Coal	Surface mining of coal	Denver Co., Colorado
	U.S. Department of the Interior (1972)	Trans-Alaska Pipeline	Oil pipeline	Alaska
	Berger (1977a, b)	Mackenzie Valley Pipeline	Gas pipeline	Northwest Territories
	Pennak (1974) Kilburn (1976) U.S.D.I.B.L.M. (1977b)	Colony Development	Oil shale development	Denver Co., Colorado
	Barton and Wallace (1978) Alberta Oil Sands Environmental Research Program (=A.O.S.E.R.P.) (1978)	Alberta Oil Sands	Tar sands development	Northern Alberta
Recreation	Foin (1977)	Yosemite	Visitor impact[b]	Yosemite National Park, California
	U.S. Department of Agriculture, Forest Service (=U.S.D.A.F.S.) (1976a)	Mineral King	Development of a new wilderness and ski area	Sequoia National Forest, California
	Montana State University (1973)	Gallatin Canyon "Big Sky"	Development of a recreation complex including skiing	Gallatin River, Montana
	U.S. Department of the Interior, National Park Service (1975)	Grand Canyon	Future use master plan[b]	Grand Canyon National Park, Arizona
Reservoirs	Geen (1975)	Moran Dam	Hydroelectric power	Fraser River, British Columbia
	Lake Winnipeg, Churchill and Nelson Rivers Study Board 1971–75 (1974)	Southern Indian Lake	Hydroelectric power	Southern Indian Lake, Manitoba
	White (1973)	Kafue Scheme	Hydroelectric power, flood control	Kafue River, Zambia
	Simmons (1972)	North Anna River	Cooling water for nuclear plant	North Anna River, Virginia
	U.S. Department of the Interior, Bureau of Reclamation (1977)	Fruitland Mesa	Irrigation	Garrison River, Colorado
	U.S. Army Corps of Engineers (1977)	Arcadia Lake	Flood control, irrigation	Deep Fork River, Oklahoma
Wastewater treatment	Skarheim et al. (1973)	Truckee River	Treated effluent	Truckee River, California
	Soltero et al. (1975)	Spokane River	Primary effluent	Spokane River and Long Lake, Washington
	Brown and Caldwell (1971) East Bay Dischargers Authority (1976)	San Francisco Outfall	Treated effluent	San Francisco Bay, California
	Jones et al. (1974)	Toguan Bay	Treated (2°) effluent	Toguan Bay, Guam
	Porcella et al. (1972)	Indian Creek Reservoir	Treated (3°) effluent	Indian Creek, Alpine Co., California
	U.S. Environmental Protection Agency (1974)	Onondaga Lake	Treated effluent	Onondaga Lake, New York

TABLE 6 (*Concluded*)

Development/activity	Reference	Descriptor	Type of project	Location
Forestry—timber management plans	Moring (1975a, b), Moring and Lantz (1975)[c]	Alsea	Alternative forest harvest practices	Western Oregon
	U.S.D.I.B.L.M. (1976)	B.L.M. - Western Oregon	Management for timber production	Western USA and Alaska
	U.S.D.A.F.S. (1978a)	U.S.D.A.-F.S. Southern California	Management for multiple use	Four national forests in southern California
	U.S.D.A.F.S. (1975)	U.S.D.A.-F.S. Shasta	Management for timber production	Shasta-Trinity National Forest, California
	U.S.D.A.F.S. (1973)	U.S.D.A.-F.S. Apache	Management for timber production	Apache National Forest, Arizona and New Mexico
	U.S.D.A.F.S. (1976b)	U.S.D.A.-F.S. Prescott	Management for timber production	Prescott National Forest, Arizona
Forestry—spraying for insect pests	U.S.D.A.F.S. (1977)	Spruce Budworm, Maine	*Choristoneura fumiferana* suppression	Maine
	U.S.D.A.F.S. (1978b)	Western Spruce Budworm	*C. viridis* suppression	North-central Washington
	U.S.D.A.F.S. and Animal and Plant Health Inspection Service (1978)	Gypsy Moth	*Lymantria dispar*	Northeastern USA
Estuarine impacts	Flint et al. (1976)	Suisun Marsh	Water diversion	Northern California
	State of California Dep. of Water Resources (1974)	Peripheral Canal Project	Water diversion	Northern California
	State of California Water Resources Control Board (1978)	Water Quality Control Plan	Water diversion	Northern California
	U.S. Army Corps of Engineers (1974)	Santa Cruz Harbor	Dredging	Santa Cruz, California
	U.S. Army Corps of Engineers (1972)	Port Hueneme	Dredging	Port Hueneme, Ventura Co., California
	U.S. Department of the Interior, Fish and Wildlife Service (1970)	Baldwin Channel	Dredging	San Francisco and San Pablo Bays, California
	Chesapeake Biological Laboratory (1970)	Chesapeake Bay	Dredging	Cheasapeake Bay, Maryland
	Battelle Pacific Northwest Laboratories (1973)	Deepwater Port	Dredging	West coast, USA
	U.S. Army Corps of Engineers (1975)	Maintenance dredging	Dredging	San Francisco Bay, California

[a]Summary report. Seven additional volumes used.
[b]Attempts to *reduce* visitor impact.
[c]Used as a model study. (See text.)

average quality, including forestry practices [1.8 (±0.2)].

Legal documents usually scored lower than others within the same development area/activity (Fig. 5). Exceptions can be attributed to greater motivation or self-interest of the people involved in the study (e.g. Toguan Bay, Grand Canyon) and/or public (political) pressure to do an adequate study (e.g. Mineral King, Peripheral Canal Project, Water Quality Control Plan). Thus, legally required e.i.a.'s need not be of inferior quality.

Additional considerations — If the Onondaga Lake, Port Hueneme, and Santa Cruz Harbor studies are representative of the main body of documents which did not even qualify for our review, then the quality of typical legal document e.i.a.'s would have to be judged as poor. It is disturbing to note that many of the legal document e.i.a.'s which were included among the best available for review scored so poorly (e.g. reservoirs: Fruitland Mesa, Arcadia Lake; fossil fuels: Decker Coal, Northwest Colorado Coal, Trans-Alaska Pipeline, Alberta Oil Sands (A.O.S.E.R.P. 1978); all of forestry practices). Are no high-quality legal e.i.a.'s available for these development areas/activities? Are typical documents even worse than those reviewed?

The Alsea study was dramatically better than the timber management plans reviewed; it could serve as a model for future e.i.a.'s of forestry practices. The team assessing reservoirs observed that the most successful studies (Moran Dam, Kafue Scheme) began by asking specific questions about ecological effects and then attempted to answer them. These two studies successfully made specific project design and operation recommendations, primarily because experimental methods were used to answer questions about the effects of

TABLE 7. Proportion of titles and documents perused chosen for review.

Development/activity	Total no. of titles perused	Total no. of reports perused	Total no. of reports chosen for review	Reviewed reports as % of titles perused	Reviewed reports as % of reports perused	Comments
Power plants	NA[a]	30	5	NA	17	One report (Atikokan) obtained by personal communication
Fossil fuels	~50	20	2	~4	10	Surface mining of coal reports. Four additional reports obtained by personal communication (See Table 6)
Recreation	NA	25	4	NA	16	
Rservoirs	NA	68	5	~<1	7	One additional report (Southern Indian Lake) obtained by personal communication
Wastewater treatment	~85	35	6	~7	17	
Forestry	~900	62	9	<1	15	One additional report (Alsea) used as "ideal" study
Estuarine impacts	~500	70	9	2	13	

[a]Not available.

alternative designs.

Although most of the best available e.i.a.'s appear to be of only average quality, individual e.i.a.'s of high quality (e.g. Truckee River, Moran Dam, Gallatin Valley "Big Sky") indicate that preparation of an excellent e.i.a. is possible.

Successes, Failures, and Future Needs of Environmental Impact Assessment

Based on the review of e.i.a.'s discussed above and an examination of the e.i.a. literature, we are able to identify successes and failures of contemporary e.i.a.'s and suggest future needs.

SUCCESSES

Public involvement — Environmental impact assessment has awakened or increased environmental awareness among the public. The apparent opening up of decision-making processes to the public (Kreith 1973; Fischer 1974; Auerbach 1977; Gamble 1978; Segree 1979) is, in large part, responsible for this (but see Fairfax 1978). Segree (1979) notes that it will take time before the effects of the recent U.S. E.P.A. public participation guidelines can be evaluated. Public participation may be an effective alternative to legal action for supervising the e.i.a. process in countries which do not have or use legal requirements for e.i.a. (Lucas 1973; Lash et al. 1974).

Public efforts and the success of these efforts varied considerably in the e.i.a.'s we reviewed. For example, public participation in power plant e.i.a.'s varied from excellent in the Seabrook study to nonexistent in the Monroe study (Table 8). Public input was significant in the Mackenzie Valley Pipeline study but was virtually ignored in the Trans-Alaska Pipeline and Northwest Colorado Coal studies. Forestry timber management plans included the public and, where public comments were incompatible with agency plans and policies, the differences were clearly noted. Perhaps the greatest asset of the legal documents reviewed was the requirement for public involvement (Fig. 3).

Environmental protection — Limited evidence indicates that environmental considerations noted in e.i.a.'s are being included along with traditional economic and engineering aspects in the development of some projects. The Decker Coal assessment process, for example, resulted in a change of project plans to preserve an ecologically sensitive area.

Research — Intriguing research problems have been elucidated and research initiated as a result of e.i.a. (Lake 1973; Lee and Wood 1978). For example, research on the effects of oil and petroleum products on northern freshwater biota (Rosenberg and Wiens 1976; Rosenberg et al. 1977; Barton and Wallace 1979; Lock et al. 1981a, b) began as part of e.i.a's of fossil fuels (Berger 1977a, b; A.O.S.E.R.P. 1978). The need for adequate monitoring and assessment of nuclear power plants led to development of the quantitative, statistically based programs suggested by Thomas et al. (1978), Gore et al. (1979), and Thomas and McKenzie (1979). The preparation of species lists, taxonomic keys, and collection of natural history information from faunistically unknown or little-studied areas (e.g. Wiens et al. 1975; Oliver et al. 1978; Barton and Lock 1979) has also been a positive result of e.i.a.'s (although maintaining a balance between this kind of activity and hypothesis-testing within an e.i.a. is important; see Table 2).

FAILURES

The list of failures of e.i.a. is, unfortunately, longer than the list of successes. As an embryonic science, e.i.a. has not progressed very far very fast (e.g. Ritchie 1978). Peterson (1974) identified three barriers to the effective consideration of ecological information in decisions to approve or reject projects. First, confusion of the roles of scientists and the public in technology assessment. The role of the scientist is to

describe objectively the changes that will probably occur; the public has to decide whether or not these changes are "bad" or "good" (see also Andrews 1973; Nielsen et al. 1973). Second, environmental costs cannot be effectively evaluated. What must be the value of preserving an area in order to equal or exceed the value of the proposed development? How extensive does environmental damage have to be in order to choose between preservation and development? "How much are nature's services worth?" (Westman 1977). Economic considerations usually will override environmental ones in a strictly analytical comparison (Peterson 1974). Third, the lack of phasing of environmental studies to coincide with industrial plans. Environmental considerations usually enter the picture too late to predict adequately the effects of a development and end too soon to assess adequately the predictions made.

Schindler (1976) identified the major failures of e.i.a. as tokenism, unrealistic time constraints, poor quality science, poor reporting procedures, and a lack of coordination among studies. Our examination of recent e.i.a.'s indicates that little change has occurred since his editorial was published (see also Kreith 1973; Burchell and Listokin 1975, p. 1). We have grouped the failures into those outside the control of the scientists doing e.i.a.'s and those over which these scientists have control. The two groups cannot be totally separated, so some overlap between them is unavoidable.

Factors outside the control of scientists doing e.i.a.'s — "Tokenism" — We observed various degrees of tokenism in the e.i.a.'s we reviewed: (i) Assessments which played no role in the fundamental yes/no decision for a project (even though regulations provide for such input), but rather were mitigative in nature; (ii) assessments which were justifications for extant engineering designs or management decisions; and (iii) assessments regarded as a necessary legal hurdle to overcome before starting the project.

i) Mitigative assessments: Peterson (1974) identified this as a general problem in e.i.a. We found it present in our review of fossil fuels, recreation, and forestry-timber management plans. For example, the Gallatin Canyon "Big Sky" study was never meant to affect the decision to develop the complex. Information generated during construction was intended as a data base for other, similar studies, and to mitigate the effect of development. The timber management plan EISs reviewed were not concerned with a cut/no-cut decision, but with best multiple use of forests while ensuring a continual yield of timber products. Adverse environmental impacts are not regarded as sufficient reason not to cut trees; alternatives are listed as mitigative actions. Thus, e.i.a. of timber management plans is limited, serving mainly as documents for interagency communication and public relations.

A major success of the Mackenzie Valley Pipeline Inquiry (Berger 1977a, b), aside from a number of innovations it presented (Auerbach 1977; Gamble 1978), was in dealing directly with the principal question: should the pipeline be built or not? (Gamble 1978, p. 951). The Berger Commission never settled for a mitigative stance.[3]

ii) Assessments as justifications: For example, the timber management plans alluded to above are primarily administrative-management documents. The forest spraying documents examined mainly concentrated on controlling pests rather than on the environmental impacts of doing so. For power plants, engineering design criteria for some projects were well established before initiation of environmental studies. Several of these documents appeared to be merely justifications for existing engineering design, perhaps reflecting: the author's opinion that appropriate environmental protection has already been incorporated in the design; hesitation by the author to suggest (or the developer to adopt) costly design changes not required by regulatory agencies; failure of predictions to identify areas where recommendations could provide effective mitigation; or a lack of understanding of design features so that appropriate recommendations for design changes could not be formulated. The legal documents reviewed by the Reservoir team (Fruitland Mesa and Arcadia Lake) also appeared to be written to justify the proposed projects. Alternatives were merely listed with no consideration of feasibility, practicality, or effects. Most of the documents examined by the Wastewater treatment team (i.e. both the literature in general and some of the studies chosen for review) primarily appeared to be justifications for projects whose design parameters had been decided before the e.i.a. was started. Many of the wastewater treatment reports reviewed confused the objectives of the proposed project with the scientific objectives of an e.i.a. Little attempt was made in the general wastewater treatment e.i.a. literature to incorporate predictive information into the design of the proposed project. Many studies merely looked for outstanding biological perturbations. That such large-scale perturbations were seldom found (usually because of inadequate methodology; see "Factors controlled by scientists doing e.i.a.'s," below) was seen as sufficient justification for initiating or completing the project. Environmental impact assessments of wastewater treatment have the advantage over other areas considered in that sewage discharges are point sources. Thus, proper predesign studies should have a better chance of lessening impacts (in this case, caused by treated effluent) than those done in other development areas.

iii) Assessments as legal hurdles: This was prevalent in the legal documents reviewed for fossil fuels and reservoirs. Nonspecific and unsubstantiated recommendations on matters not discussed or discussed only in a cursory manner in the report appeared in the reservoir assessments. Titles such as "Cumulative effects on fish" were followed by a description of how far from the project endangered species had been found (Fruitland Mesa). The Southern Indian Lake reservoir study had adequate lead time before impoundment and diversion, but had no input into the decision (already made) or even mitigation. Significant public suggestions were even ignored in two of the legal reports reviewed by the Fossil fuel team (Trans-Alaska Pipeline, Northwest Colorado Coal). Timber management plans and some of the reports reviewed for estuarine impacts also appear to be done mainly to satisfy NEPA requirements.

[3]The reader should be aware that the overall success of the Mackenzie Valley Pipeline Inquiry is being challenged. There is concern about the political nature of the Inquiry and doubt about its objectivity (Lotz 1977; Ritchie 1978). The validity of at least the environmental part of the proceedings is being challenged as there may have been some deliberate distortion in presenting and evaluating evidence on environmental problems (Ritchie 1978).

TABLE 8. Project assessments (0 = not done but should have been; 1–5 = poorly to excellently done. NA = insufficient information or element did not apply).

Development/activity and descriptor[a]	Element									
	Within scientist's control					External to scientist's control			Other	
	Def'n of scientific objectives	Back-ground prep'n	Identif. of main impacts	Predict. of effects	Usable recom-mendations	Monitoring/ assessment	Sufficient lead time	Use of recom-mendations	Public partici-pation	Adequate funding
Power plants										
Seabrook	3	3	5	4	5	NA	3	NA	5	NA
Quad-Cities	5	4	3	3	3	5	3	NA	3	NA
Atikokan	4	4	5	3	2	NA	3	NA	3	NA
Monroe	3	4	5	3	1	3	2	NA	0	NA
Ferguson	4	3	3	3	2	5	3	NA	1	NA
Sherburne	2	3	1	1	0	NA	3	NA	1	NA
Fossil fuels										
Decker Coal[b]	1	3	4	2	3	NA	3	NA	3	NA
Northwest Colorado Coal[b]	2	3	3	2	3	NA	3	NA	3	NA
Trans-Alaska Pipeline[b]	1	3	3	1	3	3	1	2	4	NA
Mackenzie Valley Pipeline	4	4	4	4	5	NA	5	5	5	5
Colony Development										
Pennak (1974) and Kilburn (1976)	4	4	3	3	4	NA	5	NA	NA	4
U.S.D.I.B.L.M. (1977b)[b]	3	3	4	3	4	NA	4	NA	3	NA
Alberta Oil Sands										
Barton and Wallace (1978)	5	4	4	4	3	2	4	NA	0	5
A.O.S.E.R.P. (1978)[c]	2	2	1	0	0	2	4	NA	0	5
Recreation										
Yosemite	5	5	4	4	2	NA	5	NA	0	NA
Mineral King[b]	3	4	3	3	2	NA	3	NA	5	NA
Gallatin Canyon "Big Sky"	5	5	5	3	4	5	3	4	3	NA
Grand Canyon[b]	3	3	2	2	4	NA	NA	NA	5	NA
Reservoirs										
Moran Dam	5	4	5	4	5	NA	5	NA	NA	NA
Southern Indian Lake	5	5	4	4	3	NA	4	NA	NA	NA
Kafue Scheme	4	4	3	4	5	NA	4	NA	NA	NA
North Anna River	3	3	4	2	3	NA	3	NA	NA	NA
Fruitland Mesa[b]	1	2	3	2	1	NA	4	NA	4	NA
Arcadia Lake[b]	0	1	1	1	1	NA	1	NA	2	NA

TABLE 8 (*Concluded*)

Development/activity and descriptor[a]	Element									
	Within scientist's control					External to scientist's control			Other	
	Def'n of scientific objectives	Back-ground prep'n	Identif. of main impacts	Predict. of effects	Usable recom-mendations	Monitoring/ assessment	Sufficient lead time	Use of recom-mendations	Public partici-pation	Adequate funding
Wastewater treatment										
Truckee River	5	5	5	4	5	NA	1	NA	NA	NA
Spokane River	5	5	5	3	2	4	NA	NA	NA	NA
San Francisco Outfall	5	4	3	3	4	3	3	3	3	NA
Toguan Bay[b]	3	4	3	3	4	NA	NA	NA	NA	NA
Indian Creek Reservoir	4	1	3	3	2	3	3	NA	NA	NA
Onondaga Lake[b]	1	3	2	1	3	NA	NA	NA	3	NA
Forestry										
Timber management plans										
Alsea	5	5	5	4	5	5	5	NA	NA	NA
B.L.M. - Western Oregon[b]	1	2	3	2	3	1	2	NA	3	NA
U.S.D.A.-F.S. Southern California[b]	2	2	2	2	3	0	4	NA	3	NA
U.S.D.A.-F.S. Shasta[b]	1	1	3	2	3	0	2	NA	3	NA
U.S.D.A.-F.S. Apache[b]	1	1	2	1	1	0	2	NA	3	NA
U.S.D.A.-F.S. Prescott[b]	1	1	1	0	1	0	2	NA	3	NA
Spraying for insect pests[b]										
Spruce Budworm, Maine	1	2	2	2	2	NA	2	NA	1	NA
Western Spruce Budworm	3	2	2	2	2	NA	2	NA	3	NA
Gypsy Moth	1	2	1	2	2	NA	2	NA	2	NA
Estuarine impacts										
Water diversion										
Suisun Marsh	2	4	4	3	4	NA	NA	NA	NA	NA
Peripheral Canal Project[b]	3	4	4	3	3	NA	2	NA	3	NA
Water Quality Control Plan[b]	3	4	3	4	4	NA	3	NA	4	NA
Dredging										
Santa Cruz Harbor[b]	0	1	2	1	2	NA	NA	NA	NA	NA
Port Hueneme[b]	0	0	3	1	2	NA	2	NA	5	NA
Baldwin Channel	4	2	4	4	0	NA	3	NA	NA	NA
Chesapeake Bay	3	2	3	3	3	NA	1	NA	NA	NA
Deepwater Port	3	2	3	2	3	NA	NA	NA	NA	NA
Maintenance Dredging[b]	3	5	4	4	2	NA	NA	NA	5	NA

[a]See Table 6 for description of documents.
[b]Legal document(s).
[c]Public relations document.

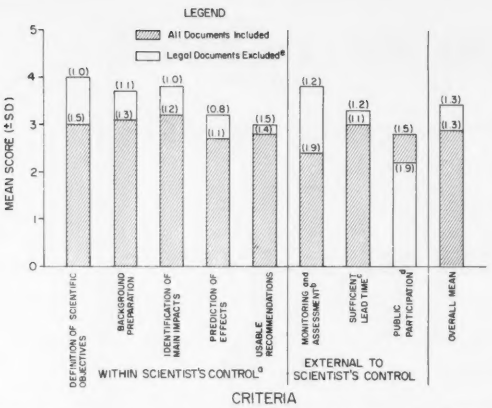

FIG. 3. Mean (±SD) scores for criteria used in assessing environmental impact documents. ("Evidence of use of recommendations" and "Adequate funding" omitted because of insufficient data. Onondaga Lake, Port Hueneme, Santa Cruz Harbor, and Alsea studies were also excluded from the calculations. See text for explanation.)

No. of documents used for averages

	All documents	Legal/publicity documents excluded
a	44	23
b	15	8
c	38	20
d	31	11
e	A.O.S.E.R.P. (1978) included with legal documents.	

Peterson (1974) observed that known sedimentary basins in northern Canada were 80% committed to petroleum exploration permits. These permits would never have been sought or granted without the assumption that, if enough reserves were found, they would be marketed. If environmental considerations were a real factor in deciding whether or when these reserves should be developed, they should have been incorporated at the permit-granting stage rather than when the company is ready to transport reserves. For example, valuable lead time was squandered in the Beaufort Sea, Lancaster Sound, and Davis Strait drilling projects, in the Canadian Arctic (Stirling et al. 1979). Government and industry are equally culpable in this regard and their strategies for doing e.i.a.'s in the Canadian Arctic have been criticized (Gamble 1979; Stirling et al. 1979). While debate between some mining and petroleum companies and the Canadian government over environmental responsibilities in the Canadian Arctic continues, development proceeds.

Unrealistic time constraints — There is widespread recognition that unrealistic time constraints (i.e. insufficient lead time, inadequate time for monitoring and assessment) seriously hamper the efficacy of e.i.a. (e.g. Baker 1978, p. 448; Petr 1978, p. 379–380). Sufficient lead time must be allowed to establish the baselines that are often a formal requirement of e.i.a.'s. Establishment of baselines requires knowledge of seasonal and long-term variations in community components

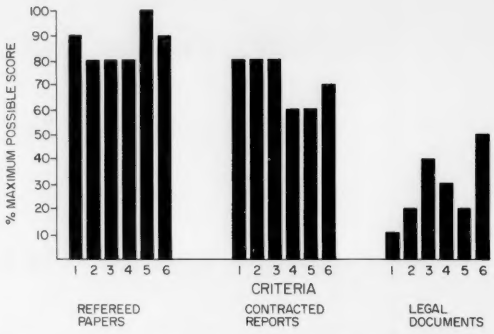

FIG. 4. Comparison of three report types used in reviewing environmental impact assessments of reservoirs. (Legend for criteria: 1 = Definition of scientific objectives; 2 = Background preparation; 3 = Identification of main impacts; 4 = Prediction of effects; 5 = Formulation of usable recommendations; 6 = Sufficient lead time. "Monitoring and assessment" and "Public participation" omitted because of insufficient data; see Table 8. Legal documents = Environmental Impact Statements prepared by U.S. Government agencies. Contracted reports = studies contracted by government agencies to research groups. Refereed papers = research studies published in primary publications and symposia proceedings.)

which, in turn, require time for study. The "....futility of rapidly determined 'base-lines'" is shown by Lewis (1980, p. 462). Insufficient lead time also creates a crisis atmosphere (e.g. see Graham et al. 1977) which is not conducive to doing effective research.

Insufficient time for postimpact monitoring, or the omission of a monitoring and assessment phase, means that predictions made are inadequately tested or not tested at all.

Our inability to evaluate the criterion "Evidence that recommendations were used in the decision or design criteria" indicates that e.i.a.'s are incomplete. Day et al. (1977) note that resource development agencies, historically, have ignored a monitoring and assessment phase[4] and that, when monitoring and assessment is done, it seldom results in changes to projects. Monitoring and assessment may be ignored by agencies because of (Day et al. 1977, p. 171): an "....emphasis on new ventures rather than past lessons...." (see also Horak and Olson 1980); an "....unquestioning commitment to particular ways of utilizing resources"; a reluctance for self-criticism (see also Sewell 1973); and uncritical attitudes of the public. Reasons for reluctance of agencies to adopt changes recommended as a result of monitoring and assessment include (Day et al. 1977, p. 176): agency "....inertia and preferences...."; increased costs; and the threat to professional reputations. Fear that e.i.a.'s will cause delays in projects is misplaced. Delays are more usually attributable to poor administration procedures and the lack of coordination in decision-making (Lee and Wood 1978) and regulatory requirements (Nagel 1978) rather than to the actual scientific research done.

[4]For example, Horak and Olson (1980) describe the laxity in monitoring and assessment by U.S. Government agencies of measures for the protection of fish and wildlife.

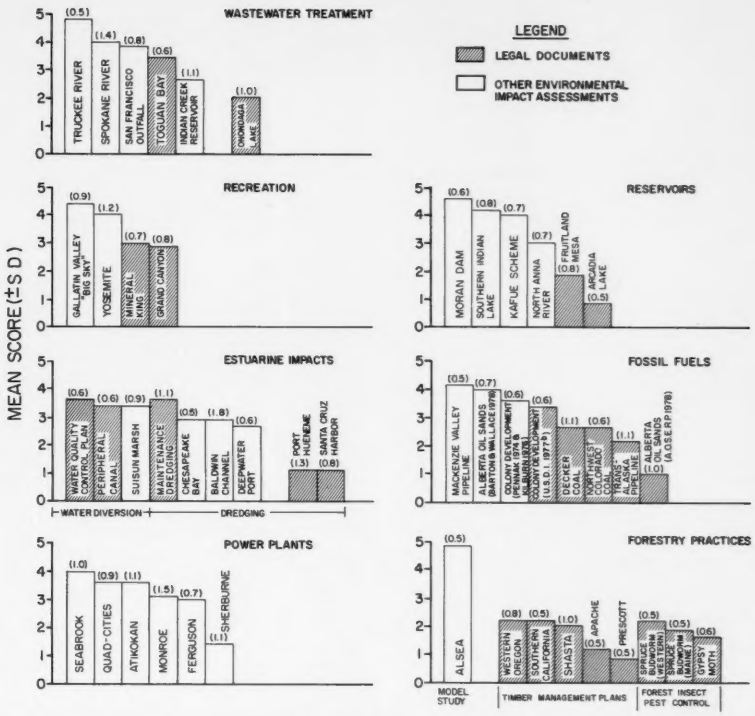

FIG. 5. Mean scores (±SD) for criteria within scientist's control for projects in each development area/activity. [Onondaga Lake, Port Hueneme, and Santa Cruz Harbor studies were chosen as typical legal environmental impact assessments and have been separated from the remaining projects. Alberta Oil Sands Environmental Research Program (=A.O.S.E.R.P.) (1978) is a public relations document and has been included with the legal documents.]

The length of lead time (all documents included) was rated as "average" (Fig. 3), with little difference apparent between legal and other documents. Lead time was inadequate in the wastewater treatment studies reviewed. Less than a single season was usually provided for on-site data collection. Most power plant projects received adequate lead time for limited biological studies but none could do the long-term studies necessary for thorough understanding of temporal variability of aquatic ecosystems. A similar concern was voiced for reservoir studies.

Petr (1978) has noted the lack of sound environmental studies for tropical and subtropical projects before the decision is made to create a reservoir. Research generally has begun after the start of dam construction[5] (e.g. Kariba Dam on the Zambezi River, Akosombo Dam on the Volta River, Brokopondo Dam on the Surinam River), and poor information exists on the conditions before damming. Such study efforts are "salvage operations" (Petr 1978, p. 371). The situation may be no better in developed countries than developing ones.

Monitoring and assessment was the most poorly satisfied of all the criteria in our review and was especially poorly done in legal documents (Fig. 3). Evaluation of this criterion was difficult because either this phase was not done or was unavailable for most reports (Table 8). In an apparent exception, monitoring and assessment data obtained for three of the six power plant projects reviewed revealed that these phases were thorough in design and scope. Similar data for the three other projects reviewed were unavailable because the plants had not been built. Elaborate laws and strict regulations for environmental protection directly govern steam electric power plants and probably explain the attention paid to monitoring and assessment of power plants. The work of Thomas and McKenzie (1979) is an example of how sophisticated the monitoring and assessment of power plants is, relative to other development areas.

Uncertainty of program or development schedules — Industry development scenarios are rarely available to people doing e.i.a.'s (e.g. Kilburn 1976); consequently "....no one sees the big picture" (Abrams and Primack 1980, p. 19). The Mackenzie Valley Pipeline, Alberta Oil Sands, and Southern Indian Lake projects are examples of this. Uncertainty creates

[5]This is a mixture of unrealistic time constraints and tokenism.

difficulties for scientists because a lack of knowledge of precise locations, schedules, processes,[6] etc. hinders development of adequate research design.

A related problem was identified in forestry-spraying programs. Monitoring done in association with spraying has been hampered by repeated changes in the areas sprayed, the chemicals used, and the dosages applied.

Industry decisions are frequently tied to market economics which can fluctuate markedly over a short time (e.g. oil), resulting in *ad hoc* planning. Activities such as development of hydroelectric power or carrying out a spraying program for forest insect pests could be more straightforward, but planners/administrators and the scientists doing the e.i.a. are not communicating effectively.

Difficult access to e.i.a. literature — Our review indicated that e.i.a. literature is usually not readily available unless a key source person or key library is found. For example, fossil fuel reports were not deposited in major libraries in the San Francisco, CA area, and were not accumulated by any cataloging or abstracting service that could be readily found. The study of recreation projects was hampered because a centralized source of case histories was lacking and desired documents were difficult to obtain. Ten-year forestry-timber management plans were available from local libraries but site-specific e.i.a.'s, required for individual timber sales, are only available from respective district offices of the U.S. Forest Service. Thus, whatever information is generated in these studies is only readily available to those directly involved in a local timber sale.

Regional E.P.A. libraries do not have complete listings of other regional E.P.A. libraries in the USA. Bibliographic publications such as EIS (a digest of U.S. Federal Government Environmental Impact Statements) and the Canadian Federal Environmental Assessment Review Process Register of Panel Projects and Bulletin only list impact studies done under NEPA and the Canadian Federal Environmental Assessment and Review Process (E.A.R.P.), respectively. When searched by the Fossil fuels team, Environment Abstracts (formerly Environment Information Access) did not contain titles of studies that were obviously predictive. INFORUM serves the specialized needs of the power industry, but how many other bibliographies exist despite our searches, or how available (within a reasonable time frame) documents listed in them would be, is unknown to us.

Questionable ethics — Reports may be unavailable to the public or may have a restricted distribution. The best available information on a project may be in special reports of state and local agencies and of consultants (Hagan and Roberts 1971). Freedom of information legislation in Canada is pending, but meanwhile, government agencies can withhold environmental information.

Anonymity of authorship precludes author accountability, a cornerstone of responsible science. For example, anonymous authorship of e.i.a.'s was encountered by teams assessing fossil fuels and reservoirs.

Designs for e.i.a.'s and reports rarely are refereed by scientists and the information contained in e.i.a.'s is published infrequently in the scientific literature. Thus, the accuracy of the contents of e.i.a.'s is questionable (Ghiselin 1975). The quality of unrefereed e.i.a.'s is frequently lower than that of refereed work as illustrated in reservoir documents (Fig. 4).

The fate of proprietary information in contemporary e.i.a. raises further ethical questions (Hanson 1976): What should be the fate of scientific but proprietary information especially if it opposes the policy of the company who paid for it? Should clients retain the right to review (and possibly suppress) scientific studies before their release to the public? Should consultants suppress results that may be unfavorable to their client? The National Association of Environmental Professionals in the USA and the Canadian Society of Environmental Biologists may serve to provide some kind of code of professional ethics which will help answer these questions.

A lack of coordination among studies — Environmental impact assessment is not developing the broad environmental overviews needed. International and intranational jurisdictional problems often result in splintering of e.i.a. effort for whole watersheds (e.g. see Munn 1977, p. 32, for remarks on the Lake Erie Basin). Results from one study are seldom applicable to other studies because they have not been planned accordingly (Schindler 1976). Considerable duplication exists and the data are generally inaccessible within a reasonable length of time, if at all (Cunningham 1973; Willis 1975). There is needless repetition in data collected at individual sites and a need for data collected on a regional basis. The statistical and design possibilities offered by a large number of regional impacts (Eberhardt 1976) go unused. Cumulative impacts of a number of major and minor projects within a region go unrecognized (Stone et al. 1973; Gamble 1979; Panek 1979). For example, what is the total effect on Hudson Bay from the diversion of the Churchill River into the Nelson River on the west (Dickson 1975; Efford 1975, table A1) and diversions of rivers into the La Grande Rivière (James Bay power development; see Penn 1975; Efford 1975, table A1) on the east (Baxter and Glaude 1980) plus other developments in the James and Hudson Bay regions? The team studying estuarine impacts-dredging noted that impacts likely to be expressed on a regional scale or as a result of chronic exposure to perturbation were infrequently assessed. A lack of coordinated data gathering in forestry-timber management plans precluded the possiblity of studying regional effects.

Factors controlled by scientists doing e.i.a.'s — The scientific failure of many e.i.a.'s can usually be attributed to poor research design. Environmental impact assessment techniques may be inadequate and the state of the art still primitive, but the scientific method is available and should be relied on more heavily. The following are examples (including development areas) of common deficiencies in design.

Poorly stated objectives (fossil fuels,[7] forestry-timber

[6]Threats to proprietary interests have probably been exaggerated (Lee and Wood 1978).

[7]Prevalent in legal documents.

management plans) *and a lack of hypothesis testing* (fossil fuels[7]) — Environmental impact assessments frequently lack an overall research plan or goal, research being planned and done in an *ad hoc* manner.

Superficiality of research — i) Lack of original research. Background work and predictions (non-quantitative) for forestry-timber management plans and spraying were largely restricted to literature surveys (the "information broker" approach of Ward 1978, p. 128) and/or case history studies.

ii) Attempts to be all-inclusive. Gore et al. (1979) suggest that monitoring of aquatic habitats is usually inconclusive because too many parameters are sampled. Baldwin (1974, in Lee and Wood 1978, p. 67) foresaw the problem: "....by making the environmental impact statement the complete economic and environmental decisional document it may become environmentally unrigorous and increasingly lengthy, unmanageable and useless for agency and public decision-making." The broad coverage attempted in forestry-timber management plans and some reservoir studies resulted in a superficial treatment.

iii) Use of generalized taxonomic classifications. This was common in forestry. Power plant studies underemphasized field reconnaissance resulting in a deficiency in breadth and quality of taxonomic determinations and, consequently, the investigation of community dynamics.

iv) Failure to consider a broad range of applicable literature. Power plant studies identified this failure and noted that while the citation of local reports is important for comparative purposes, other sources of information are necessary for broad understanding of potential environmental effects. Reservoir studies found that this shortcoming pertained to legal documents which only used in-house reports, technical bulletins, and EISs.

v) Poor support of statements by inadequate referencing (recreation, fossil fuels, forestry; see also Priddle 1977).

Inadequate use of predictive techniques — i) Heavy reliance on surveys to the exclusion of experimental manipulation and/or modeling (fossil fuels, reservoirs, recreation, wastewater treatment). Inordinate amounts of time, effort, and money are spent collecting specimens and cataloging data (the "busy taxonomist approach" of Ward 1978, p. 127; see also Brink 1978; Knetsch and Freeman 1979; Cooper and Zedler 1980), and insufficient time is devoted to testing hypotheses in e.i.a. (Ward 1978). The "busy taxonomist approach" is based on the mistaken premise that "....knowing what is present in the system and perhaps something about how it operates in its current state will allow us to guess how it will operate when changed by development actions" (Ward 1978, p. 127; see also Holling 1978). Recent guidelines for e.i.a.'s often require establishment of baselines (e.g. Manitoba Environmental Assessment and Review Support Services et al. 1978), exacerbating the situation (Knetsch and Freeman 1979). Profuse amounts of undigested data overwhelm reviewers and decision-makers with unimportant detail, inhibiting formulation of conclusions and well-informed decisions on a proposal (Flamm 1973). Effects observed in case history studies are often deemed pertinent to a particular e.i.a. without even cursory field checks (e.g. estuarine impacts). Reliance on inferential evidence to suggest causation does not explain cause and effect pathways. Experimentation would allow identification of causal pathways and improve the predictive abilities of e.i.a.'s (see Table 2). The Wastewater treatment team noted a lack of site-specific experimental manipulation to determine the effects of toxicants and biostimulants on organisms in receiving waters. Only limited amounts of species-level toxicity data are available and few species are sufficiently widely distributed to be common to most project sites. Therefore, on-site bioassays are necessary (e.g. Truckee River, see Skarheim et al. 1973). The only example of modeling attempted in the reservoir studies examined was based on hydrological and postoperational information but not biological data.

ii) Lack of quantitative data (recreation, forestry). Even when sufficient data seemed to be available, recreation reports did not make quantitative predictions concerning changes to be caused by proposed projects.

Poor statistical design — Gore et al. (1979) concluded that most monitoring programs for nuclear power plants were not designed with statistical analysis in mind or for detecting change. Lack of sound sampling design, inconsistent data collection, and changing procedures made many of the preoperational sampling programs inadequate (see also Horak and Olson 1980). In the reservoir studies reviewed, no control conditions were established and no attempts were made to account for variance in baseline data. Selection of sampling sites was often based more on convenience than on ecological rationale. Physical and biological data were often collected at grossly different times, thus precluding the possiblity of even obtaining correlative evidence.

Indirect and cumulative impacts are poorly studied — Estuarine impact and forestry studies reviewed, especially, appeared to be confined to short-term, direct, acute, and local effects. Indirect, long-term, cumulative impacts are usually neither identified nor studied. The Wastewater treatment team suggested that effluent bioassays should measure the effects of individual components of effluent and their synergistic/antagonistic effects. Further, several trophic levels should be included to yield information on effects at the community level.

Poor organization of reports (reservoirs, estuarine impacts) — Use of impractical formats hindered extraction of valuable information and communication of primary messages.

Implications — The immediate failures of e.i.a. may be less important than the long-term effects of these failures (from Schindler 1976): a decline in credibility of environmental science and scientists; reduction in the quality of scientific personnel involved in e.i.a.; and degradation of our natural resources "....because of the ineffectual groping of environmental scientists."

Future Needs

In this final section, we propose corrections for some of the failures discussed above and identify needs for future research in e.i.a. The treatment is divided into organizational/administrative needs (largely outside the control of those actually doing e.i.a.'s) and scientific/research needs (largely within the control of those doing e.i.a.'s.

Organizational/administrative needs

Improved access to e.i.a. literature — Well-publicized comprehensive bibliographies and central depositories for reports from e.i.a.'s are needed. Therefore, we recommend:

i) Expansion of a publication such as "EIS" to include all required (statutory and non-statutory) e.i.a.'s done in North America and not currently listed (e.g. state and city projects on nonfederal land; e.i.a.'s undertaken privately and/or with a research motivation). A *complete* catalogue of e.i.a.'s is needed.

ii) A single, comprehensive, computer-based, on-line, abstracting service for e.i.a.'s should be developed. Currently, Environment Abstracts is accessible on-line but EIS only sells computer searchable tapes.

iii) Environmental impact assessment reports should be advertised and distributed to major libraries and other public institutions [e.g. National Technical Information Service (NTIS), Springfield, VA] across the continent. Documents should be available through the mail in all regions of the USA and Canada. In this regard, the Alberta Oil Sands Environmental Research Program (A.O.S.E.R.P.) has instituted mailings of publication announcements, monthly information circulars, and reports, all of which contain information on availability of A.O.S.E.R.P. reports (e.g. see Smith 1979). Reports are also sent to a number of libraries. The Alaskan Outer Continental Shelf Environmental Assessment Program (OCSEAP) distributes its reports to >300 addressees (Engelmann 1979). Its reports are available from NTIS and its data products are available from Environmental Data and Information Service, Boulder, CO (Engelmann 1979). If successful, these systems could serve as models for other long-term environmental impact studies.

iv) Follow-up documents should be kept with the original, predictive e.i.a. so that the entire package is readily available. This would include results of monitoring and assessment during and after the project, and evidence of how recommendations from the original report have been used (e.g. Horak and Olson 1980) (see below).

Increased accountability for e.i.a.'s and their authors — i) Final project decisions/designs should be described and available [see (iv) above] so the reader can evaluate use of the original recommendations. Detrimental impacts resulting from ignoring (or accepting!) recommendations, and avoidance of detrimental impacts because recommendations were followed should also be identified (Horak and Olson 1980).[8] In this way, e.i.a. can be made more exacting and accountability can be increased.

ii) Environmental impact assessments should be signed by their authors rather than being anonymous opinions submitted by their employers (Templeton 1974). Just as there should be no secrecy surrounding information generated in e.i.a.'s, the authors of these documents must be identified. This would do much to bring "....environmental reports under the same scholarly standards which both guide and protect basic research and its practitioners" (Ghiselin 1975, p. 264).

iii) Environmental impact assessments should be subjected to peer review to improve their quality. Auerbach (1977, p. 23) suggested that "With large projects, new and more adversarial methods of 'peer review' should perform a similar function" (cf. Berger 1977a, b). This may require a reduction in the number of e.i.a.'s done to avoid swamping the peer review system.[9] Individual researchers would be well advised to circulate, unofficially, their preliminary designs for e.i.a.'s and draft reports to colleagues for critical comment. Publication of at least parts of e.i.a.'s in the primary scientific literature would improve accountability of the authors and also make the data available to a larger audience.

Improved public input into project decisions and designs — There is a need for *effective* public involvement in e.i.a. (e.g. Nagel 1978; Abrams and Primack 1980). Methods to do this are discussed by Abrams and Primack (1980) for making decisions on management of radioactive wastes from power plants, and Erickson (1980) for natural resource agency decision-making (see also Canter 1977; Erickson 1979). Livingston (1980) notes that effective input of environmental information into the education of children is also important. Adequate philosophies and methods hopefully will be developed to handle relevant public concerns as a result of inclusion of the public in the e.i.a. process.

Proponents should encourage public input to all stages of e.i.a. The Mackenzie Valley Pipeline study was a model of public involvement (Auerbach 1977; Gamble 1978). Proponents can acquire data, opinions, and recommendations useful in decision-making. Public commentary and suggestions should be encouraged and incorporated early enough, where applicable, to affect the outcome of a project (Emond 1978; Erickson 1979).

Improved preparation of e.i.a. reports — We recommend that the organization and format used in scientific publications be adopted. Documents prepared to fill legal requirements suffer from the requirement to follow a standardized organizational format without consideration of scientific methodology. These guidelines frequently result in obfuscation rather than clarification. For example, presentation of vast amounts of data impedes the logic of the recommendations made. The data should be placed in accessible appendices where they can be referred to, if desired. Continued production of voluminous documents of undigested material will only serve to reduce effectiveness of e.i.a. reports. Other recommendations include:

i) A summary to be placed at the beginning of the doument.

ii) The use of effective visual presentations throughout the text. Tabular and graphical presentation of results, alternatives, recommendations, etc., can promote more effective communication (e.g. Canter 1977; Brink 1978; Holling 1978; Engelmann 1979).

iii) Complete referencing of material used in the report so the reader can obtain information relating to the assumptions and limitations of the data used (Canter 1977; Priddle 1977; Erickson 1979).

[8]Dorney (1977) suggests that cost savings or additions that can be legitimately identified as resulting from e.i.a. should be documented (see also Horak and Olson 1980).

[9]A reduction in the numbers of e.i.a.'s and an increase in the quality of those done would be a worthwhile goal.

iv) Predictions made should clearly indicate the predictive techniques used (Erickson 1979) and the data obtained.

v) Recommendations should be clearly stated to allow their separation from other possible but unlikely or undesirable alternatives (e.g. Brink 1978). Specific, feasible recommendations should be made on items directly pertinent to design and operation of the project.

Scientific / research needs — "....We cannot afford to permit the operation of a sort of Gresham's law in ecological work in which mediocre and topical research would prevail over more rigorous, soundly based environmental studies, if indeed the requirement for impact studies is to live up to its philosophical implications" (Hedgpeth 1973, p. 443). We "....must seek to put....[our]....studies on a scientifically credible basis — to see that problems, terms of reference, funding, time constraints, reports, and conclusions are all within a bona fide scientific framework" (Schindler 1976).

Development of methods to define and quantify relationships between biological, aesthetic, and economic impacts, for use in decision-making (e.g. Sewell 1973; Lash et al. 1974; Munn 1975; see also Cooper and Zedler 1980) — Our review has not emphasized this aspect of e.i.a. (cf. p. 609) because of its highly specialized nature. This approach may be important in combatting "tokenism." Environmental impact assessment has often created animosity, causing polarization of opinion and action. Neither a statutory requirement for e.i.a. (e.g. USA) nor a non-statutory system which strongly recommends e.i.a. (e.g. Canada) have successfully changed attitudes toward e.i.a. Thus, tokenism probably will never be eliminated, but it may be moderated, in time, especially if barriers to effective consideration of ecological information in decisions to approve or reject projects are removed. Effective evaluation of esthetic preferences and environmental intangibles would help remove such barriers.

There is also a need for value judgments and their implications to be made explicit in e.i.a.'s to allow for their scrutiny (Matthews 1975; see also Lash et al. 1974; Templeton 1974; Brink 1978; Erickson 1979; Straus 1979). Subjective decisions and value judgments are always part of e.i.a., either being required during the course of an e.i.a. (e.g. selecting types of impact for study, deciding on the acceptability of impacts, etc.) (Matthews 1975; Van Winkle et al. 1976) or in the evaluation of esthetic preferences and environmental intangibles as part of an e.i.a. (e.g. Harger and Culhane 1974; Randall et al. 1974). These subjective judgments are based on values, feelings, beliefs, and prejudices and are functions of the personal, institutional, and societal contexts of the analyst (Matthews 1975). The ecologist, in supplying predictions of potential impact, must be as scientifically sound and objective as possible, but in recommending acceptability of a predicted impact he should recognize his role as a citizen-professional and that his recommendations reflect his own value system (Van Winkle et al. 1976).

Support for biological inventory programs independent of e.i.a.'s — "....We must constantly improve the data-base, so that we develop a capability not only to know and say what we have, but also to detect processes and change" (Polunin and Eidsvik 1979, p. 23). There is no doubt that the availability of previously collected background data improves the quality of e.i.a. (especially when lead time is short).[10] However, e.i.a.'s should focus on predicting the effects of a proposed development rather than using valuable time (usually in short supply) doing necessary background work (e.g. initial faunal and floral surveys, preparing species lists, etc.). This kind of survey information could be provided by groups such as the Illinois Natural History Survey (Smith 1977), the European Insect Survey (Heath 1971), and the recently formed Biological Survey of the Insects of Canada (Entomological Society of Canada 1974; Danks 1979). Environmental impact assessments could proceed without the enormous encumbrances of developing preliminary data if such North American organizations could, for example, develop data bases (including identification guides) in areas of the USA and Canada which have been understudied and which face massive new developments. An institutional base wider than the needs of individual projects is required, implying some form of government sponsorship (Cooper and Zedler 1980). The Federal Environmental Assessment and Review Process in Canada at one time indicated some government financial support for environmental baseline studies (Hurtubise 1977, p. 1), but only limited support has materialized either within government departments or for groups like the Biological Survey project. (In fact, mention of Canadian government support for environmental baseline studies is omitted from Federal Environmental Assessment and Review Office 1979).

Data storage and retrieval programs associated with a national effort at surveying the biota (identifying species and mapping their distributions on a country-wide basis) and updating natural and man-made changes in the biota (Cooper and Zedler 1980) are monumental undertakings but necessary if the data collected is to be usable. The BIOSTORET system in the USA eventually may be useful in this regard. Some attempt should be made to coordinate cataloging and retrieval of faunal and floral data from regional e.i.a.'s that have been completed. Voucher specimens collected in the course of an e.i.a. should be lodged in appropriate museums or universities for future reference (Resh and Unzicker 1975; e.g. Engelmann 1979).

Adequate time frames for e.i.a.'s — "....The scheduling and phasing of the development activities must reflect the time required to obtain and assess adequate environmental information" (Fischer and Davies 1973a, p. 225). Peterson (1974) noted that comprehensive environmental studies do not begin with or before geophysical exploration in the Canadian north — one reason that environmental data are not advanced to the point where they can be used for trade-off analyses in decisions on whether or not the last phase (transportation) of oil and gas development should occur. Necessary ecological studies should be done in phase with exploration — about a decade lead time is reasonable for both (Peterson 1974). Provision of adequate lead time would do

[10]For example, studies of estuarine impacts in the San Francisco Bay–Delta region scored above average because of the detailed ecological studies previously conducted in the area.

much to reduce the tokenism apparent in many contemporary e.i.a.'s. Environmental impact assessment must be given the time to prove that it can help, rather than hinder, developments. Adequate lead time still exists in many areas which eventually will be developed (e.g. see Livingston 1980).

Improved design of research — Environmental impact assessment should be considered a research problem and designed accordingly. Key questions should be asked, hypotheses formed, and research designed to test these hypotheses. Conclusions should follow directly from the results of hypothesis testing. Research should focus on prediction and subsequent assessment of effects. To this end, we recommend that:

i) Predictive techniques (especially experimental manipulations and modeling) be emphasized (e.g. Thomas et al. 1978; Holling 1978; Ward 1978; Gore et al. 1979). During an e.i.a. the collection of baseline data should not be an end in itself; rather, baseline data collected should function as part of an experimental/predictive approach (Cooper and Zedler 1980). "....All data and information collected should be utilized for making actual predictions" and "....new data should only be generated when the data are required for making predictions and when they are not already available from other sources...." (Erickson 1979, p. 93–94). Likewise, a research design that optimizes the usefulness of case history studies should be adopted (e.g. Hall et al. 1978). Further refinement of experimental manipulation and modeling techniques will do much to enhance the quality of e.i.a.

ii) Use of statistical techniques in the design and analysis of e.i.a. research be improved and that those improvements be used more frequently in e.i.a. For example, useful statistical approaches to monitoring and assessment are discussed in recent papers by Green (1978), Thomas et al. (1978), and Gore et al. (1979). The latter two papers consider the following practical matters involved in monitoring nuclear power plants: concentrating sampling on important species rather than sampling everything (see also Resh 1979); sampling design with statistical analysis in mind, or to detect change; the use of paired stations in the sampling design (see also Hall et al. 1978); adequate duration of preoperational sampling (usually at least 2–3 yr); allocation of initial sampling effort (to suit the period of maximum abundance of organisms, or when critical life stages are present) and final sampling effort (a stopping rule so field monitoring does not continue indefinitely and resources can be reallocated to other work); and stability of design over time. An intriguing approach to monitoring effects of mining activities on wildlife is presented in Chapter 15 of Holling (1978).

Inclusion of monitoring and assessment in every e.i.a. — This need was almost unanimously identified by the assessment teams involved in this review. Despite the difficulties involved (Table 2), monitoring and assessment is necessary during construction and after project completion to indicate excessive impacts for immediate mitigation (and provide regulatory information for environmental management); to validate predictions of short- and long-term impacts; to provide data and experience useful to prevent or mitigate impacts in future projects which are similar;[11] to yield recommendations regarding operational schemes (e.g. reservoirs); to provide data on higher-order (secondary, tertiary, etc.) cumulative or indirect effects of development on ecosystem structure and function;[12] and to provide a dynamic basis "....for revising policy and techniques, perhaps repeatedly" (White 1980, p. 188; see also Holling 1978; Erickson 1979; Horak and Olson 1980). Design of an adequate monitoring and assessment program should be done early in the e.i.a. (Holling 1978; Engelmann 1979; Horak and Olson 1980).

The use of ecological reserves as control sites for monitoring and assessment of environmental impacts is a sensible suggestion (e.g. Franklin et al. 1972; Jenkins and Bedford 1973; Peterson 1973; see also Kilburn 1976; Hinds 1979).

Study of cumulative impacts on a regional, national, or international basis (e.g. Environment Protection Board 1973; Lash et al. 1974; Duffy 1975; Willis 1975; Holling 1978; Erickson 1979; Gamble 1979; Panek 1979; Stirling et al. 1979; Thomas and McKenzie 1979; Cooper and Zedler 1980) — There is a need to evolve from the single site orientation of most e.i.a.'s to a study of concurrent impacts from several unrelated proposed projects within a region and to document the mutual and cumulative impacts of these simultaneous developments. "Every project, no matter how small, should be viewed in a regional setting" (Cooper and Zedler 1980, p. 286). White (1980) stresses the importance of using a holistic framework in finding solutions to environmental problems. Holistic approaches using natural areal units (e.g. watersheds) rather than politically established borders are needed in e.i.a. Similarly, biospheric impacts on a global level (e.g. carbon dioxide, freons) deserve coordinated international attention. Incremental treatment of projects can neglect the effects of a number of projects within a discrete geographical area (e.g. water diversions in coastal estuarine areas; multiple reservoir development in a single watershed). A single project may have no measurable impact(s), but a number of these within a region may exert significant effects (e.g. Craig et al. 1979; Panek 1979; Cooper and Zedler 1980). The following strategies are available: (i) synthesis of data from site-specific e.i.a.'s with a view to identifying cumulative impacts; (ii) use of models general to a number of sites [e.g. plankton simulation models may be general to a number of sites and joint data collection for parameter estimation over a region may therefore be possible (Swartzman 1979)]; and (iii) increased coordination, cooperation, and communication between existing projects. Regional data centers may be able to reduce redundant efforts and maximize data collection efficiency for e.i.a.'s. For projects covering vast areas (e.g. pipeline construction), use of ecological reserves established along the route (see above) may provide the necessary information.

Improved communication between scientists and planners — Scientists need access to development schedules or programs

[11]For example, studies of recreational developments are severely hampered by the lack of accumulated data on previous ecology of an area and on the effects of visitor use.

[12]For example, long-term cumulative impacts resulting from widespread use of insecticides for forest insect pests are generally unknown and were not addressed by e.i.a.'s we examined.

to optimize research plans. This may not be possible when proprietary information is involved although, where a genuine risk to security and commercial interests is involved, sensitive information is probably presentable in a way that avoids the problem (Lee and Wood 1978). However, in more straightforward situations (e.g. scheduling of water level changes in reservoirs, spraying programs for forest insect pests) there is no reason why planners and scientists should not communicate more effectively.[13] Alternatively, scientists could lessen their dependence on this kind of information by developing experimental strategies applicable to a wide range of situations rather than relying on situation and site specificity.

Acknowledgments

The Freshwater Institute granted D. M. R. a Career Development Leave to teach the graduate seminar which led to this report. We thank E. Sylvester, E. Schlinger, and the Division of Entomology and Parasitology, University of California, Berkeley, the University of California Water Resources Center (Project UCAL-WRC-W-519), and OWRT Project No. A-063-CAL for their support. R. McV. Clarke, D. G. Cook, A. L. Hamilton, R. J. Livingston, D. P. Scott, and J. R. Vallentyne reviewed drafts of the manuscript and provided useful comments. P. Emond and S. K. Fairfax provided background on Canadian and U.S. environmental law, respectively. W. R. Effer and E. B. Peterson provided documents and/or useful suggestions for our review. R. T. Seidner gave us permission to use draft copies of A.O.S.E.R.P. reports. A. P. Wiens helped at all stages in the production of the manuscript. L. Taite drafted the figures. K. Vitt and D. Laroque typed drafts of the manuscript.

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[13]Abrams and Primack (1980) describe a successful Swedish exercise in holistic planning of the management of radioactive wastes from nuclear power plants. This approach would be valuable in doing away with the piecemeal nature of many e.i.a.'s.

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CJFSDX38(5) 485–626(1981)
ISSN 0706-652X

Volume 38, No. 5, May 1981 Volume 38, nº 5, mai 1981

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